INFLUENCES OF CLIMATE VARIABILITY AND LANDSCAPE MODIFICATIONS ON WATER DYNAMICS, COMMUNITY STRUCTURE, AND AMPHIPOD POPULATIONS IN LARGE PRAIRIE WETLANDS: IMPLICATIONS FOR WATERBIRD CONSERVATION

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DOCTOR OF PHILOSOPHY

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ABSTRACT

Northern prairie pothole wetlands provide crucial habitat for numerous waterbirds. However, wetland abundance and quality in the Prairie Pothole Region of North America has declined because of agricultural landscape modifications. Effective management of waterbird populations relies on understanding how landscape modifications alter wetland hydrology and biological communities in context of climate-driven wet–dry periods.

A common modification involves consolidation of smaller more-temporary wetlands into larger more-permanent ones. I evaluated whether consolidation drainage has progressive-chronic effects on hydrology of remaining wetlands during 2003–2010 in the Prairie Pothole Region of North Dakota. For wetlands in topographic basins that were not already full, rate of water surface area change was positively correlated with consolidation drainage during a wetting phase, but negatively correlated during a drying phase. This unbalancing of water budgets through wetting and drying phases suggests that 1) consolidation drainage has a progressive-chronic effect on wetland hydrology; and 2) wetlands receiving water in extensively drained landscapes will continue to increase in volume through each climate fluctuation until they reach their spilling point, then stabilize. Proportion of wetlands covered by cattail was negatively correlated with increases in water depth, thus cattail coverage may increase as water levels stabilize as a result of consolidation drainage. Fish were present in 57% of wetlands and probability of fish occurrence was greater in wetlands that had greater water depth and wetland connectivity. Weak evidence suggests amphipod densities decreased where there was extensive drainage and increased in more full basins, probably due to improved overwinter survival.

The alternative stable states hypothesis predicts clear versus turbid observable states that reflect differing trophic structures in wetlands. I conducted a landscape-scale evaluation of this

hypothesis by examining the distribution of remotely-sensed chlorophyll *a* concentrations within 978 wetlands. My findings suggest that trophic structure in prairie wetlands is better understood within a continuum of trophic status rather than discrete states. My results provide an improved understanding of how land use and climate variability influence productivity in wetlands across the region and should help shape future research and conservation priorities focused on wetland services and waterbird populations.

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CHAPTER 1. GENERAL INTRODUCTION

Northern prairie pothole wetlands provide crucial migration and breeding habitat for numerous waterbirds, including fourteen species given Level-I and Level-II Conservation Priority under the North Dakota Comprehensive Wildlife Conservation Strategy (NDGF 2004). Effective management and restoration of wetland habitats targeted toward species of conservation priority relies on an understanding of how land use can alter wetland hydrology and ultimately influence the biological community structure and productivity in wetlands. Land-use changes must be understood in context of climate variability, because fluctuations between wet and dry conditions drive wetland hydrology in the Prairie Pothole Region (van der Valk 2005).

Hydrologic fluctuations in response to climate variability have shaped floral and faunal community structures of prairie pothole wetlands for thousands of years (Kantrud et al. 1989; Laird et al. 2003). Productivity in prairie pothole wetlands pulses in response to nutrient cycling that is driven primarily by inter-annual water-level fluctuations (Murkin 1989; Euliss et al. 1999). Semipermanent wetlands are especially important across a region that experiences pronounced wet–dry climate fluctuations. During dry years they may offer the only suitable habitat for waterbirds in the region, while during wet years these wetlands are capable of producing great amounts of food resources that support a variety of higher level consumers (e.g., waterbirds, salamanders, and fish; Kantrud and Stewart 1984; Batt et al. 1989; Kantrud et al. 1989; Euliss et al. 1999; Anteau and Afton 2009a; Anteau 2012). Accordingly, disturbances in wetlands that alter hydrologic responses to climate variability represent a threat to native communities and productivity. Moreover, abundance and quality of prairie wetlands has declined due to landscape modifications, primarily related to agriculture (Dahl 1990; Anteau and

Afton 2008; Bartzen et al. 2010; Anteau and Afton 2011), and these declines may ultimately impact waterbird populations (e.g., Devries et al. 2008; Anteau and Afton 2009b).

Since the late 1800's, demand for agriculture in the northern prairie regions of the United States has resulted in conversion of 75–99% of native prairie uplands for agricultural land use and other development (Samson and Knopf 1994), with drainage of >50% to ~90% of the original wetlands (e.g., North Dakota and Iowa, respectively; Dahl 1990). Consequently, the quality of many remaining wetlands has been reduced due to hydrologic modifications and sedimentation (Euliss and Mushet 1996; van der Kamp et al. 1999; Anteau 2012). Tillage within a catchment may increase hydroperiods of less-permanent wetlands, but likely has less of an effect on the hydrology of more-permanent wetlands that primarily receive water input from groundwater (Euliss and Mushet 1996). However, drainage of smaller, less-permanent wetlands into larger, more-permanent ones (i.e., consolidation drainage) represents a threat to all wetland communities where it occurs (Krapu et al. 2004; Anteau 2012; McCauley et al. In Review). Consolidation drainage moves water from many sites in the upper portion of the catchment to a single site at the bottom of a catchment. Consolidation drainage likely minimizes recharge of groundwater, decreases evapotranspiration that would normally occur in the upper catchments (Spaling and Smit 1995; Anteau 2012), and disrupts hydrologic fluctuations in remaining wetlands in response to climate variability (Merkey 2006; Anteau 2012). Thus, wetlands that hold consolidated water are larger now than they were historically (McCauley et al. In Review). Furthermore, wetlands in highly drained catchments are more likely to spill over their topographic basin to become further connected to wetlands in adjacent basins (Leibowitz and Vining 2003). I examined the impact of consolidation drainage on water-level dynamics in

more-permanent wetlands in North Dakota during both a climatic drying phase and a wetting phase (Chapter 2).

Changes in hydrologic fluctuation and wetland connectivity have the potential to influence ecological communities in prairie wetlands. High and stable water regimes may shift community composition toward species adapted to more hydrologically stable environments. Further, increased connectivity among basins often provides colonization corridors for aquatic-obligate species (e.g., fish) that rarely colonize isolated basins (Peterka 1989). Together these conditions can favor certain invasive plant and animal species like cattail (*Typha* spp.) and fish that can further threaten natural ecological functions in prairie wetlands. Those species were historically kept in check in native communities by greater dynamics and surface isolation of natural wetlands (Shay et al. 1999). Compared to historical records the prevalence of cattails and fish was found to have increased in prairie wetlands in 2004 and 2005, at the end of a high and stable water regime (Swanson 1992; Anteau and Afton 2008). These increases likely have implications for habitat structure and abundance and quality of forage for waterbirds. Therefore, I evaluated how landscape modifications and water-level dynamics have influenced the abundance and distribution of cattail and fish in prairie wetlands of North Dakota (Chapters 3 and 4).

Aquatic invertebrates are an important component of the waterbird food resources produced in prairie wetlands (Euliss et al. 1999). Agricultural landscape modifications have been linked to decreased abundance of aquatic invertebrates or shifts in community composition that may alter food availability (Euliss and Mushet 1999; Anteau et al. 2011). In prairie wetlands, amphipod density can serve as an indicator of wetland and water quality because amphipods are sensitive to contaminants, disturbances in uplands, and invasive species (Grue et

al. 1988; Tome et al. 1995; Duan et al. 2000; Anteau and Afton 2008; Hentges and Stewart 2010; Anteau et al. 2011). In a 2004–2005 survey, amphipod density was low across the Prairie Pothole Region (including North Dakota) compared to historical records (Anteau and Afton 2008), perhaps due to landscape modifications (Anteau and Afton 2008; Anteau et al. 2011). However, amphipod densities could have been low because 2004–2005 was preceded by a period of relatively high and stable water since 1993 (Euliss et al. 1999; Euliss et al. 2004). The Prairie Pothole Region in North Dakota experienced moderate to severe drought during 2006–2008 (NCDC 2014), making it possible for basins to have lower water levels and subsequent nutrient cycling (Euliss et al. 1999). In spring 2009, wet conditions returned to prairie wetlands in North Dakota (NCDC 2014). During 2010–2011, I surveyed amphipods within the same North Dakota wetlands surveyed in 2004–2005 (Anteau and Afton 2008), and evaluated changes in their density in relation to water-level dynamics and landscape modifications (Chapter 5). By comparing water-level data and amphipod densities collected in 2010 and 2011 to those collected in 2004 and 2005, I intended to provide, 1) an estimate of amphipod densities available for spring-migrating and pre-breeding waterbirds under climatic conditions expected to be better for amphipod production, and 2) an understanding of how landscape modification effect the influence of climate variability on hydrology, amphipod density, and overall wetland productivity.

Scheffer et al. (1993) described two alternative states in shallow lakes (typically <3 m depth; Scheffer 1998), a clear state where primary productivity is dominated by submerged aquatic vegetation and a turbid state where primary productivity is dominated by phytoplankton (hereafter the “alternative stable state” hypothesis). Both semipermanent wetlands (Kantrud et al. 1989) and shallow-water permanent wetlands (i.e., shallow lakes; Scheffer et al. 1993) have

been reported to exist in either a clear or a turbid state (Bayley and Prather 2003; Zimmer et al. 2009). Communities where submerged aquatic vegetation is abundant generally have food webs with higher density and greater diversity of both invertebrates and vertebrates than in phytoplankton-dominated wetlands (Hargeby et al. 1994; Scheffer and van Nes 2007). Aquatic invertebrates, typical in clear wetlands, are important prey for waterbirds of conservation concern. Consequently, clear-water wetlands likely provide better foraging conditions for waterfowl and other waterbirds than do turbid wetlands (Anteau and Afton 2008). I evaluated the alternative stable state hypothesis by examining whether these clear versus turbid states were observable across landscapes in the Prairie Pothole Region of North Dakota as indicated by a bimodal distribution of wetland chlorophyll *a* concentration (Chapter 6). To conduct the evaluation across landscapes, I assessed previously published remote sensing techniques (see Sass et al. 2007) and developed new indices to estimate chlorophyll *a* concentrations as a proximate estimate of phytoplankton biomass within large semipermanent and permanent prairie wetlands (Chapter 6). I examined the distribution of wetland chlorophyll *a* concentrations for evidence of bimodality or discontinuity. Finally, I evaluated the influence of landscape modification on wetland chlorophyll *a* concentration by applying both a continuous model and a binomial model based on response thresholds consistent with the alternative stable states hypothesis (Chapter 6).

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CHAPTER 2. PRIOR CONSOLIDATION DRAINAGE HAS PROGRESSIVE-CHRONIC EFFECTS ON WETLAND HYDROLOGY

Abstract

The potential of legacy effects from past ecosystem disturbances to progressively degrade ecosystem integrity in the absence of management intervention has been ignored in ecological literature. Identifying the temporal influence of a disturbance is essential to understanding how ecosystems respond to environmental change and to developing management strategies. I used drying and wetting phases resulting from climate variability during 2003–2010 in the Prairie Pothole Region of North Dakota as a natural experiment to evaluate whether past wetland drainage has progressive-chronic effects on the hydrology of 122 remaining, more-permanent wetlands. For wetlands in topographic basins that were not already full (due to lower watershed connectivity), the rate of water surface area change was positively correlated with past drainage of wetlands within catchments of focal wetlands during the wetting phase, but was negatively correlated during the drying phase. Wetlands that were nearer their spilling point changed less during each phase than those basins that were less full. This unbalancing of water budgets through wetting and drying phases suggests that wetlands in extensively drained landscapes will continue to get larger through each climate fluctuation until they reach their spilling point; then water levels should stabilize and produce a sustained, non-isolated lake phase. Accordingly, past wetland drainage in the catchment likely has progressive-chronic effects on the hydrology of more-permanent wetlands in the region. These changes in wetland hydrology have implications for the integrity of ecological systems and social benefits derived from wetlands in the region. Further, my findings support the hypothesis that wetland drainage increases surface-water transfer from smaller to larger watersheds, adding to landscape- and regional-scale flooding

problems. Lastly, my results illustrate the importance of understanding the temporal influence of anthropogenic disturbances for making informed conservation decisions, because progressive-chronic effects can continue to degrade ecosystem services unless the prior disturbance is mitigated.

Introduction

Anthropogenic modifications to landscapes can have long-lasting effects on ecosystems, and those effects can remain well after disturbance events are over. Accordingly, to understand how specific disturbances contribute to environmental change both an appropriate spatial and temporal scale of observation are required to avoid misinterpretation of the effect or non-effect on ecosystem response (Allen and Starr 1982). Much attention has been given to the accumulation of anthropogenic modifications across a landscape or through time (Weller 1988; Turner II et al. 1990; Spaling and Smit 1995). However, a scientific understanding of long-term, or legacy, effects that disturbances have on ecosystems, even after further disturbance ceases remains somewhat elusive (Harding et al. 1998; Foster et al. 2003; Cuddington 2011; Martin et al. 2011). Identification of the temporal influence of an anthropogenic disturbance in an ecosystem is a critical piece of information for conservation programs to understand, because there is potential for further ecosystem degradation as a result of inaction if the past disturbance continues to progressively affect the ecosystem.

Effects of ecosystem disturbances can manifest as temporally acute or chronic. An acute effect will cause a temporary change in the condition of the ecosystem, and then once the disturbance has ceased, resilience within the system can return the ecosystem to the previous condition (Holling 1973; Figure 2.1)—akin to an allostatic response mechanism (Sterling and Eyer 1988). Alternatively, chronic effects may keep ecosystems in a changed state. However,

simply stopping future modifications to a landscape may not be enough to stop the increasing ecological effect of the disturbance. While static-chronic effects cause a more-immediate transition to a new stable state (Scheffer et al. 2001), some disturbances may create a positive feedback mechanism that may continue to amplify deleterious effects on an ecosystem after the disturbance has ceased (Figure 2.1). Borrowing from epidemiology, I term these effects as progressive-chronic effects. Temporal scale is important in distinguishing between progressive- and static-chronic because eventually progressive-chronic effects may appear as static-chronic effects once a system fundamentally changes in structure and function.

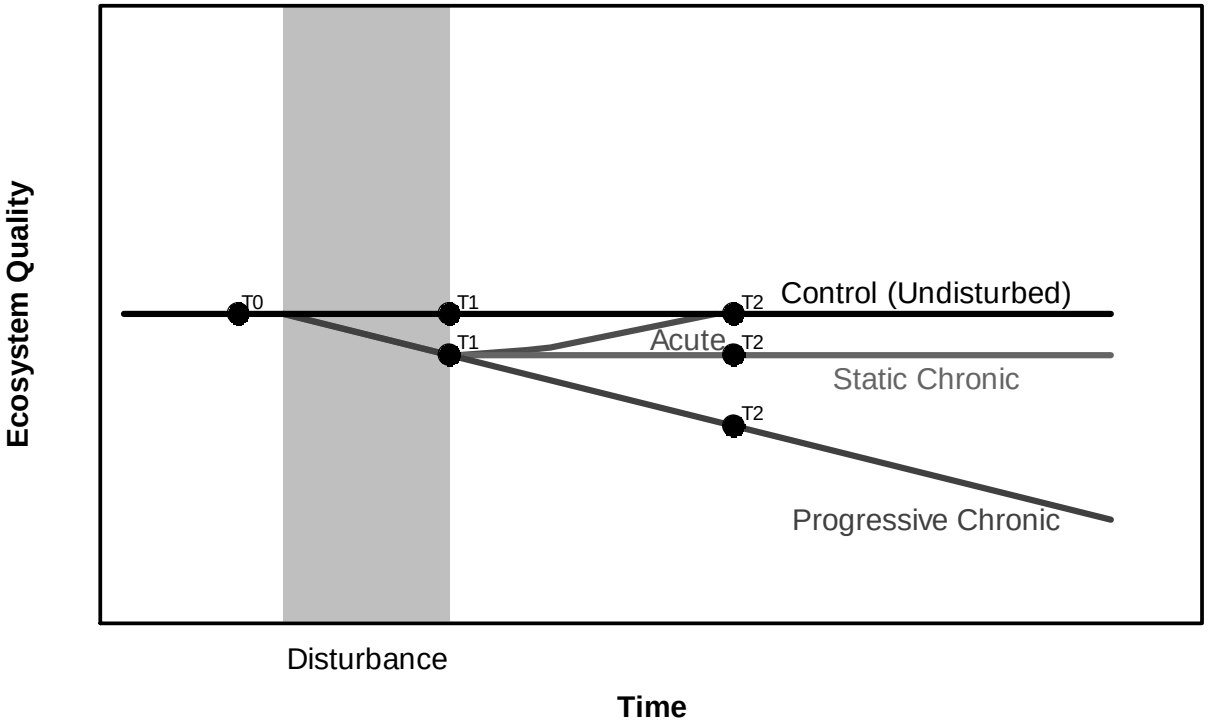

Figure 2.1. Conceptual model of possible temporal influences (acute, static-chronic, and progressive-chronic) that a disturbance can have on quality of an ecosystem over time. T0, T1, T2 represent a generic ecosystem quality prior to, immediately following, and some time after the disturbance event, respectively.

Wetlands in the Prairie Pothole Region of North Dakota have experienced a number of ecological disturbances during the recent past (1970s to present), which makes this an ideal area for examining the temporal influence of disturbances related to land use. Namely, consolidation drainage is a common practice used by some agricultural producers throughout the region in an attempt to increase tillable acreage. The practice involves draining smaller, less-permanent wetlands into larger, more-permanent ones (Krapu et al. 2004; Anteau 2012). Recent studies have demonstrated that wetland water levels historically responded more strongly to climate variability than they do currently (Post van der Burg et al. In Prep.), and that wetlands with increasing consolidation drainage in their catchment had increased size compared to their historical size (McCauley et al. In Review). In prairie pothole wetlands, hydrological, biophysical, and biological processes are driven by periodic wet–dry climate periods (Winter and Carr 1980; Batt et al. 1989; Kantrud et al. 1989; Laird et al. 2003); therefore, disturbances that change hydrological responses in wetlands to climate variability can alter their ecology and potentially reduce their value in providing services to society (Poiani and Johnson 1993; Johnson et al. 2010; Anteau 2012; McCauley et al. In Review).

While it is now known that consolidation drainage that occurred historically has had a chronic effect on remaining wetlands (McCauley et al. In Review), it remains unclear if that disturbance continues to degrade the hydrological responses of those wetlands to climate variability. Where consolidation drainage has occurred there is an increased rate of surface water flow from the upper to the lower portion of the catchment. Thus, wetlands in the lower catchment would have altered hydrologic responses characterized by increased surface water in-flow during both wetting and drying climate phases. Further, wetlands that collect consolidated water likely dry less quickly because surface area to volume ratios may decrease and result in a

reduction of evaporation (Winter 1989) and because there is less groundwater infiltration in larger wetlands (van der Kamp and Hayashi 1998). If consolidation drainage has indeed had a progressive-chronic effect on wetland hydrology, there is a potential for further ecosystem degradation to occur as a result of management inaction in highly modified catchments. Thus, temporal influence of a disturbance is an important piece of information for conservation programs to use in prioritizing efforts to improve efficacy of the programs.

Here, I present a natural experiment that examines the temporal influence of wetland drainage on the hydrology of remaining wetlands in the Prairie Pothole Region. Based on the work of McCauley et al. (In Review), I focused on the most recent climate period (2003–2010) that included a drying and a wetting phase of similar intensity. Selection of this time period limited the potential complications of changes in the amount of catchment drainage between or within climate phases, because consolidation drainage in my study area predominantly occurred prior to 2003 (McCauley et al. In Review). This framework allowed me to use separate tests of catchment modification as a progressive-chronic effect on water level dynamics in each climate phase to form my interpretation of the overall effect on wetland hydrology response to climate variability.

If consolidation drainage has had a static-chronic effect on wetland hydrology, the observed water level response within wetlands during wetting and drying phases should not be dependent upon the amount of consolidation drainage in the catchment and respond similarly to wetting and drying events (Figure 2.2). However, if consolidation drainage has a progressive-chronic effect, then hydrologic responses to wetting or drying phases would be dependent upon the amount of consolidation drainage in the catchment (Figure 2.2). I consider this a progressive-chronic effect because variation in hydrologic response occurred when I detected no

change in the amount of drainage throughout the study period. Further, if wetland response to wetting and drying phases differed in amplitude, attributable to drainage, this would also indicate progressive-chronic effects.

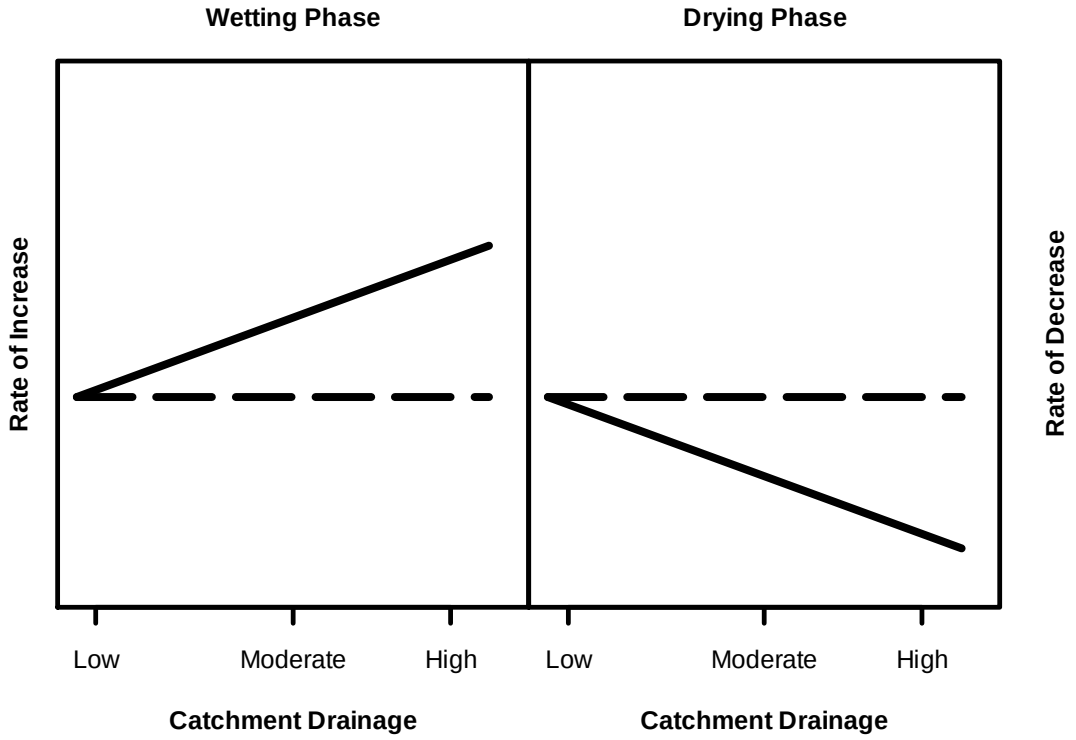

Figure 2.2. Predictions of experimental results under the expectation that catchment drainage has a progressive-chronic effect on rate of change in water surface area in remaining more-permanent wetlands during climatic wetting and drying phases (solid line). This prediction is compared to the expected result if catchment drainage did not affect the rate of change, but had either an acute effect, or a static-chronic effect (dashed line).

Methods

Study Area

My study area was the Prairie Pothole Region of North Dakota (Figure 2.3) where wetlands of varying water permanence (hereafter, hydroperiods) have formed within glacially-created depression basins that were historically surrounded by temperate grassland. In these wetlands, hydrological, biophysical, biological processes are driven by periodic wet–dry periods caused by an oscillating climate pattern (Winter and Carr 1980; Batt et al. 1989; Kantrud et al. 1989; Laird et al. 2003). Larger and more-permanent wetlands were of particular interest in this study because their condition is affected by disturbances throughout a larger watershed area that often includes multiple smaller, less-permanent wetland basins; therefore, larger, more-permanent wetlands may indicate the condition of the landscape (Anteau and Afton 2011).

Accordingly, I studied lacustrine semipermanent and shallow-water permanent wetlands (Cowardin et al. 1979) that were originally randomly selected by Anteau and Afton (2008; n = 153) and visited once in 2004 or 2005. Wetlands must have had an open water area larger than 120 m across to be surveyed in 2004 or 2005. In 2004 or 2005, if reselection in the field was necessary, the nearest suitable semipermanent or permanent wetland was surveyed. In 2010 and 2011, I was able to return to and collect necessary data from 122 of the original 153 wetlands. Based on National Wetland Inventory classification (NWI; U.S. Fish and Wildlife Service 2003), 67% of wetlands were semipermanent, 3% seasonal, and the rest were permanent wetlands or shallow-water lakes. Those wetlands classified by NWI as seasonal were reselected wetlands that were more characteristic of semipermanent wetlands at the time of the field assessment in 2004 or 2005.

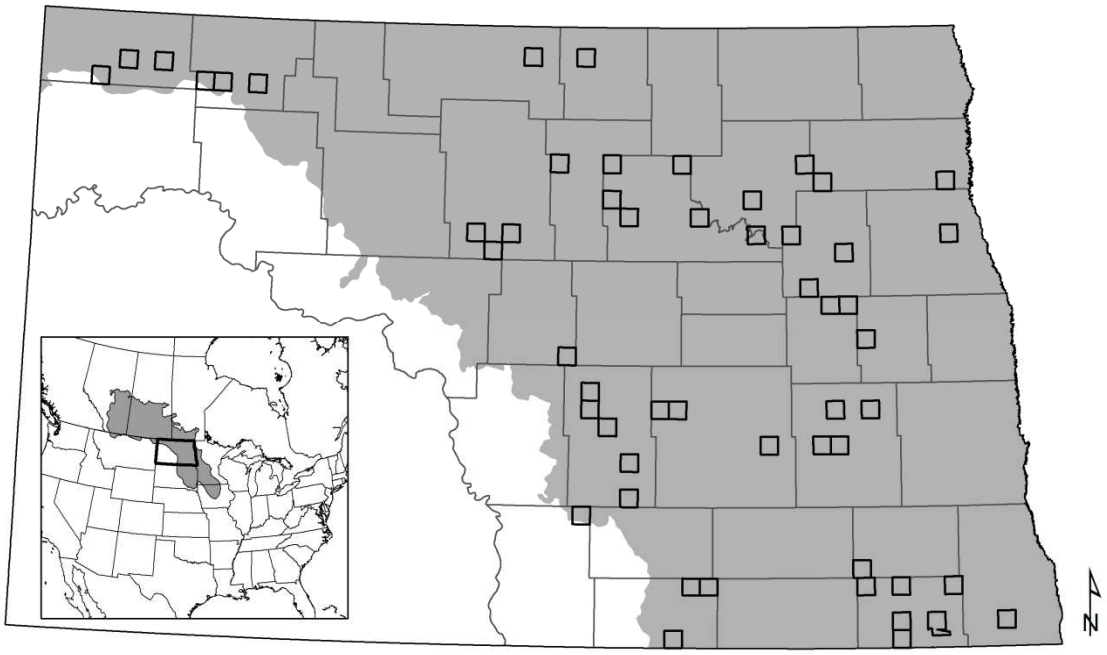

Figure 2.3. North Dakota study area with Prairie Pothole Region shaded, counties east of the Missouri River outlined, and randomly selected townships outlined wherein three wetlands were randomly sampled. Inset map of the United States and Canada showing the location of the Prairie Pothole Region (shaded) and North Dakota (bold outline).

Data Preparation

Climate index

I used a fine-scale climatic wetland hydrologic index (2.5 arc-minute) derived by Post van der Burg et al. (In Prep.) to estimate the effect of climate on water surface area within wetlands using the standardized precipitation-evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) calculated from PRISM (Parameter-elevation Regression on Independent Slopes Model) Climate Group data (PRISM Climate Group 2002; Di Luzio et al. 2008). SPEI can summarize moisture surpluses or deficits by aggregating the difference between precipitation and potential evaporation over different time scales. During the period of my study, uniformly averaged monthly climate conditions over the previous six years best explained wetland water

levels (Post van der Burg et al. In Prep.). Index values above zero represent wetter climate conditions and values below zero represent drier conditions.

Based on climate conditions, I designated 2003–2005 as a wet period, 2006–2008 as a dry period, and 2009–2010 as a wet period. I then identified the drying phase as the change between the first wet period and the dry period, and the wetting phase as the change between the dry period and the second wet period. I structured my analysis of wetland surface area change by these two climate phases. In North Dakota, there is geographic variability in 1) the amount of variability in the difference between precipitation and evapotranspiration, and 2) the intensity of wetting and drying phases during one period of time (Laird et al. 2003; Post van der Burg et al. In Prep.). In my model, I controlled for the influence of geographic variability in the intensity of wetting and drying phases by using the peak-to-peak amplitude of the climatic wetland hydrologic index for each phase.

Catchments

I used wetland catchments defined by McCauley et al. (In Review) that were delineated using high-resolution digital elevation models (DEM) to detect the portion of the landscape where surface water flows into the focal wetland. These catchments were an index of watershed derived wetland complexes that included more-intermittent wetlands and their catchments (McCauley and Anteau 2014). DEM source data included 1 m pixel lidar (data available from the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR; Intermap Technologies, Inc., Englewood, Colorado). I used catchment size in my analysis, but I also used the extent of the catchment to define the area to assess land use effects upon wetlands (McCauley and Anteau 2014). For logistical reasons associated with assembling landscape variables, such as amount of wetland area drained, I used catchments truncated to a 2.5 km

maximum radius from the wetland basin for 46% of catchments because they were large or highly irregular in shape. The 2.5-km radius encompassed >90% of the total catchment area for 68% of catchments. Landscape conditions within these 2.5-km truncated catchments should represent the condition of the full catchment, and the conditions nearest the wetland basin likely influence the basin most. Therefore, I assume the 2.5-km-truncated catchment provided a reasonable area to evaluate impacts of land use in this system and are an improvement over the simply buffering around a wetland a set distance, a common practice (McCauley and Anteau 2014).

Catchment drainage

I used estimates of the percent of the catchment area that was drained wetland during 2003–2010 from multiple data sources, including: aerial photographs, DEM, NWI, and spatially explicit soil data (see McCauley et al. In Review). Wetlands were identified as drained if they were present in historical photographs (dating back to 1937) but not present in current photographs, or if the wetlands were identified as part of a drainage network. Significant drainage occurred prior to 2003 in my study area; however, I found negligible evidence of additional drainage after 2003.

Basin area

Within a catchment, I defined the basin as the topographic depression that collects surface water and which is isolated from basins of other wetlands of an equal or more permanent hydroperiod. I calculated the maximum potential water surface area of each basin using the high-resolution DEMs (3 m pixel lidar or 5 m pixel IfSAR) to find the elevation at which water flows out of the basin (i.e., spill point) and then delineated the area at that spill point elevation within the basin. Because I predicted that wetlands in basins that were near full or that were full

would have less surface area dynamics, I calculated the proportion of the basin that the focal wetland filled at the start of each climate phase. I used a logit transformation of the proportion-basin-full variable × 0.1 for use in my analysis.

Water surface area

I delineated water surface area for each surveyed wetland by photointerpretation of National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture) aerial imagery for 2003–2006 and 2009–2010 (McCauley et al. In Review). Photointerpretation was performed while images were viewed as panchromatic instead of true-color, because they were done as part of a larger study that involved panchromatic imagery (see McCauley et al. In Review). Where the waterline was obscured by emergent vegetation, the waterline was approximated to be halfway between the emergent-vegetation to open-water interface and clearly identifiable upland. NAIP imagery was not available for 2007 and 2008. For those years I used wetland water surface area delineated once in either 2007 or 2008 using high-resolution digital elevation model (DEM; source data: 1 m pixel lidar; Data available from the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR) orthorectified image (Intermap Technologies, Inc., Englewood, Colorado).

I calculated the rate of increase in water surface area for each wetland during each climate phase as the natural logarithm of the quotient of final surface area divided by the initial surface area. For this calculation I used the maximum surface area from the wet period and the minimum surface area from the dry period. The rate of increase was useful as a response variable in my model because it allowed me to evaluate temporal dynamics, in a way that is similar to that used in population biology (Hastings 1997).

Maximum depth

Depth of a wetland, along with topography (see Bank Slope below), can be used to describe wetland basin shape and how water volume is distributed within the basin. To account for the relationship of surface area and depth, I measured water depth (±0.1 m) at four locations in each wetland. Locations were along randomly selected transects at 60 m from the shoreline or emergent vegetation ring toward the center of the wetland. I used the maximum observation from the initial survey in 2004 or 2005 in my analysis.

Bank slope

I calculated the bank slope of each wetland because I expected water-volume-to-surface area relationships to differ with varying bank slopes. Wetlands with steeper sides would have smaller changes in surface area with added volume than wetlands with flatter sides. I recorded the average elevation of the water surface for all wetlands in 2007 or 2008 (the driest years) and in 2010 (a wet year) using high-resolution DEMs. I calculated the average radius of each wetland polygon in 2007 or 2008 and 2010 using surface area calculations of each wetland (radius = $\sqrt{\text{area}/\pi}$). I calculated bank slope as change in water surface elevation from 2010 to 2007 or 2008 divided by the change in radius from 2010 to 2007 or 2008. On average, 2010 was a wetter year and water levels were higher than in 2007 or 2008 but in those rare cases (~5%) where 2010 water levels were actually lower than in 2007 or 2008, another wetter year was substituted.

Land use

I indexed current agricultural impacts within the catchment by calculating the proportion of the upland that was cropland (i.e. row crop or small grains). Each quarter-quarter section (~16 ha) within the catchment was classified as cropland if ≥50% of the upland area was determined

to be cropped from photointerpretation of 2003 or 2004 NAIP imagery (see McCauley et al. In Review).

Statistical Analyses

I tested whether catchment drainage had a progressive-chronic effect on the rate of surface area increase within wetlands during a drying phase and a wetting phase. In my analysis, I was primarily interested in a catchment-drainage-by-climate-phase interaction. If the hydrologic response is dependent upon the amount of consolidation drainage in the catchment then the slope of the model fitted line should be different from zero indicating a progressive-chronic effect (Figure 2.2). McCauley et al. (In Review) found a positive relationship between wetland size and consolidation drainage in the catchment when examining within wetland variation from historical to current eras. However, I found no support for correlation between wetland water surface area at the start of each phase and amount of consolidation drainage in the catchment ($|r| < 0.01$), which indicated that wetland size was not already confounded by drainage in my random sample of wetlands that had high variation in size.

I used mixed-effects regression analysis to evaluate the influence of catchment-drainage-by-climate-phase interaction on water-level change (lme4 package in R statistical computing environment; R Development Core Team 2010; Bates et al. 2011). I evaluated covariate suites within my *a priori* model by comparing versions of the model created with all combinations of covariates suites (16 combinations). Covariate suites included: hydrogeomorphic (logit transformed proportion basin full, catchment-drainage-by-basin-full interaction, and initial water depth), geomorphic (log of bank slope and log of catchment area), land use (percent cropland), and climate (change in climate index during the phase). I did not find evidence of collinearity among continuous fixed effect variables within the full model ($|r| \leq 0.26$). I also included an

interaction of each covariate by climate phase because I expected the rate of increase to be of opposite sign between climate phases. I identified wetland as a random error term to account for the repeated measure across climate phase and to ensure proper variance estimates for fixed effects of all models. I interpreted and made predictions from the most parsimonious combination of covariate suites, which I evaluated by the number of estimated parameters and Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). I evaluated model goodness-of-fit using the squared correlation coefficient (r^2) between observations and model fitted values. Confidence intervals for fixed effect estimates were calculated at the 85% level to best match criteria used during covariate suite selection using AIC_C (Arnold 2010).

I plotted the effect of catchment drainage on the rate of increase during the wetting phase and rate of decrease (rate of increase × –1) for the drying phase separately for three levels of basin full. I sliced the basin full variable at the 25th, 50th, and 75th percentiles, representing less full, moderately full, and near full, respectively. I plotted the predicted effect of catchment drainage on rate of change (increase or decrease, appropriately) for wetlands for a spectrum of percent basin full to illustrate the degree of net balance in water budgets through drying and wetting phases. For the drying phase I plotted effect estimates for 3–90% of basin full, representing the 1st to 75th percentile of my data, because this range represents wetlands that would likely remain isolated from downstream surface water connections throughout the drying phase. For the wetting phase I plotted effect estimates for 1–34% of basin full, representing the 1st to 25th percentile of my data, because these wetlands remained below the spill point throughout the wetting phase; therefore, the estimates were not influenced by water spilling out of the basin. Additional covariates were set to median values in all effect plots.

Results

My analysis included a total of 122 wetlands of which catchment sizes ranged from 4–200,900 ha and the mean was 3,686 ha (median = 394 ha). Percent of catchment area that was drained wetland ranged from 0–13% (median = 1.1%). Basin area ranged from 1.7–6,646 ha and the mean was 182 ha (median = 34 ha). On average, at the start of the drying period basins were 67% full (SD = 27, 25th percentile = 51% full, median = 67% full, 75th percentile = 90% full) and at the start of the wetting period basins were 53% full (SD = 27, 25th percentile = 34% full, median = 50% full, 75th percentile = 73% full). Percent of upland that was cropland averaged 52% and ranged from 0–100% (median = 55%). The mean wetland water surface area was 65.4 ha (SD = 129. 8, median = 24.5 ha) during the two wet periods and 54.7 ha (SD = 118.2, median = 17.4 ha) during the dry period. My climate index ranged from -1.6 to 2.0. Mean climate index for each period was different from zero in the expected direction for the climate period (Figure 2.4). The mean differences in climate index were -0.83 (SE = 0.03) and 0.89 (SE = 0.04) during the drying and wetting phases, respectively.

My final model of wetland surface area dynamics included the treatment effect of catchment-drainage-by-climate-phase interaction, hydrogeomorphic and climate covariate suites, and the random error term (Table 2.1). My model explained 52%, 13%, and 51% of the variability within the observations overall, within the drying phase, and within the wetting phase, respectively. Model parameter estimates are reported in Table 2.2. Catchment drainage when focal wetland basins were less full was positively correlated with rate of increase in water surface area during the wetting phase and negatively correlated with rate of decrease in water surface area during the drying phase (Figure 2.5A). Catchment drainage was not correlated with rate of water surface area change during either the drying or wetting phase where focal wetlands

moderately filled their basin (Figure 2.5B). Catchment drainage when focal wetland basins were nearly full was negatively correlated with rate of increase in water surface area during the wetting phase and positively correlated with rate of decrease in water surface area during the drying phase (Figure 2.5C). The rate of change in wetland surface area became increasingly different between the drying and wetting phases with increased catchment drainage (Figure 2.6).

Discussion

My results indicate that past wetland drainage in a catchment can have a progressive-chronic effect on drying and wetting phases of remaining wetlands and potentially on overall wetland hydrology throughout the Prairie Pothole Region. This effect appears to manifest itself in an unbalancing of wetland water budgets, which culminates in a pattern of increasing wetland size over consecutive wet–dry climate fluctuations. This result indicates that the full impact of historical wetland drainage has not yet been realized and that further degradation of wetland ecosystems is likely because catchment drainage appears to influence succession of remaining wetlands toward lake-like hydroperiods, as wetlands grow to and maintain at their spill point elevations. This finding is a significant piece of information that could inform decisions about wetland restoration, because inaction will lead to further degradation of semipermanent wetland ecosystems. Here, I propose a mechanism by which to explain previously observed trends that indicate an increase in the size of wetlands compared to historical size within drained catchments (McCauley et al. In Review).

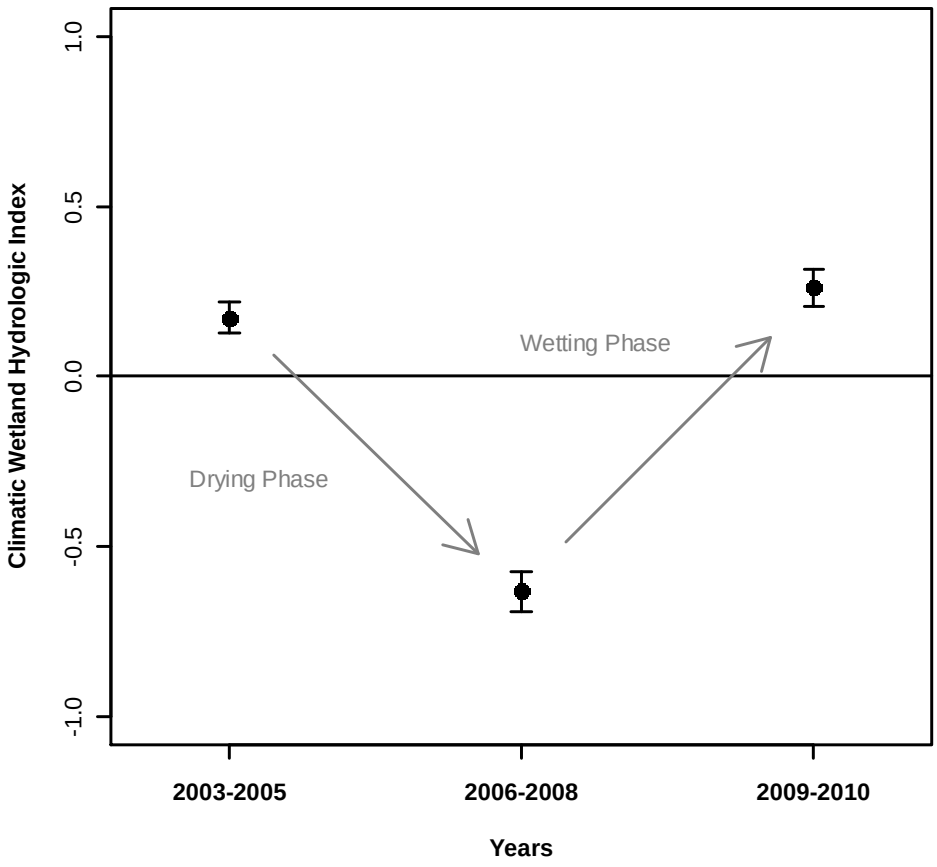

Figure 2.4. Mean standardized precipitation-evapotranspiration climate index values and 95% confidence intervals from all surveyed wetlands for each climate period of the study. A value above zero to be a wet period and a value below zero to be a dry period. Arrows (gray) indicate the climate phases between climate periods.

Table 2.1. Covariate suite selection results from an *a priori* model used to examine the effect of catchment drainage on water-level dynamics in wetlands of North Dakota during a drying and a wetting phase, included are: model log likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small sample size (AIC_C), increase over lowest AIC_C (ΔAIC_C), and Akaike model weight (w_i) for combinations of covariate suites ($w_i \geq 0.01$).

Covariate Suites	LL	K	AIC_C	ΔAIC_C	w_i
Hydrogeomorphic, Climate	-118.78	13	265.15	0.00	0.45
Hydrogeomorphic, Land Use, Climate	-116.76	15	265.64	0.49	0.35
Hydrogeomorphic	-122.70	11	268.55	3.40	0.08
Hydrogeomorphic, Land Use	-120.51	13	268.59	3.44	0.08
Hydrogeomorphic, Geomorphic, Land Use	-117.56	17	271.83	6.68	0.02
All Covariate Suites	-115.44	19	272.27	7.12	0.01
No Covariate Suites	-166.54	6	345.43	80.28	0.00

Table 2.2. Estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 85% confidence limits for fixed effects within the most parsimonious model used to examine the effect of catchment drainage on water-level dynamics in wetlands of North Dakota during climatic drying and wetting phases. A colon indicates an interaction between variables.

Fixed Effects	$\hat{\beta}$	SE	LCL	UCL
Intercept	-0.0444	0.1947	-0.3247	0.2360
Catchment Drainage	-0.2392	0.0427	-0.3006	-0.1777
Basin-Full	0.1457	0.0546	0.0671	0.2243
Maximum Depth	0.2412	0.0537	0.1639	0.3185
Climate	0.2200	0.0981	0.0787	0.3612
Wetting Phase	0.0489	0.2638	-0.3309	0.4288
Catchment Drainage : Wetting Phase	-0.0158	0.0209	-0.0460	0.0143
Basin-Full : Wetting Phase	-0.2235	0.0646	-0.3165	-0.1305
Catchment Drainage : Basin-Full	-0.0901	0.0162	-0.1135	-0.0668
Maximum Depth : Wetting Phase	-0.3389	0.0770	-0.4498	-0.2280
Climate : Wetting Phase	-0.0588	0.1373	-0.2564	0.1388

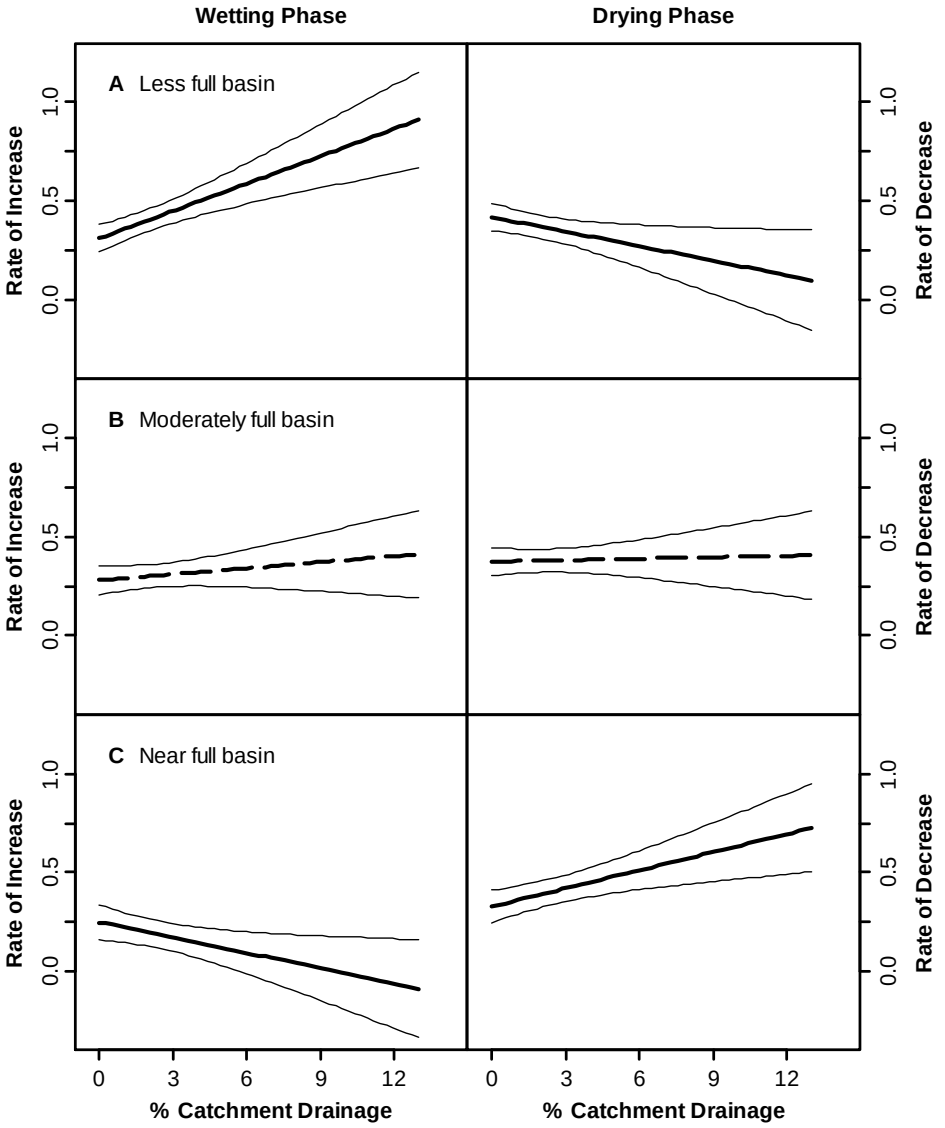

Figure 2.5. Model predicted effects of past wetland drainage on the rates of increase and decrease in wetland water surface area (85% confidence intervals) derived from observations of semipermanent and permanent wetlands in North Dakota during a recently wet–dry climate fluctuation. Predictions were made for focal wetlands that were (A) less full, (B) moderately full, and (C) almost full, determined by 25th, 50th, and 75th percentiles of the data for the drying phase (51%, 67%, and 90%), and for wetting phase (34%, 50%, and 73%), respectively. Solid lines represent estimates with a slope different from zero and dashed lines represent estimates with a slope not different than zero.

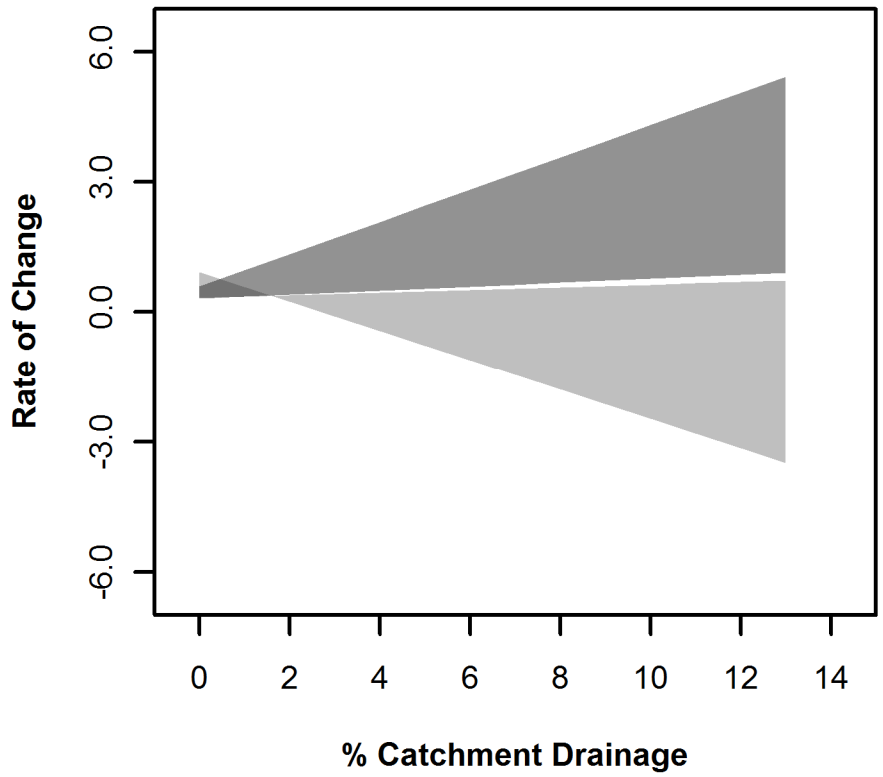

Figure 2.6. Model predicted effects of past wetland drainage on the rate of change in wetland water surface area over a spectrum of basin fullness values for remaining focal wetlands derived from observations of semipermanent and permanent wetlands in North Dakota during a recent wet–dry climate fluctuation. The drying phase is represented by the lighter gray color and wetting phase by the darker gray color. Predictions for the drying phase were plotted over a range of less to moderately full basins (3–90%), because this range represents wetland dynamics less likely to be influenced by artificial drainage pathways in the upper portion of the basin. Predictions for the wetting phase were plotted over a range of less full basins (1–34%), because these wetlands remained below the spill point throughout the wetting phase. Wetland water budgets are interpreted to be unbalanced where rate of change estimates do not overlap.

In this natural experiment, I considered wetlands with <1% of the catchment area drained (n = 58) a control group. I observed similar dynamics between the drying and wetting phases for wetlands with minimal drainage, which supports the notion that each climate phase I examined had similar magnitude of influence on wetland hydrology. However, the water budget within wetlands were increasingly unbalanced across drying and wetting phases where previous

drainage in catchments was >2% of area. I suspect that wetlands receiving consolidation drainage water from historical drainage efforts will continue to increase in size with each subsequent wetting phase, until they reach their spill point and then stabilize. This effect is most evident in wetlands that have not yet filled to their natural or artificial spill point. Whereas, in wetlands that were more full the rate of increase in water surface area decreased during the wetting phase and the rate of decrease in water surface area increased during the drying phase, likely due to water spilling out of the basin through either the natural or artificial spill points. My observations support the hypothesis that consolidation of wetlands leads to semipermanent and permanent wetlands in drained catchments experiencing a successional change toward a more lake-like condition which likely has regional-scale implications on both the integrity of wetland ecosystems and social benefits derived from services provided by wetlands (Anteau 2012).

This natural experiment demonstrates a case where legacy effects on ecosystems can continue to degrade the integrity of an ecosystem after a disturbance activity has ceased and that lack of management action likely will result in further deterioration of ecosystem function. Identification of historical drainage of wetlands within the catchment of remaining wetlands could inform the prioritization of conservation efforts to initially focus on remediation of wetlands that have not yet reach their basin spill points, and restoring complexes of less-permanent wetlands in the upper catchment to improve surface water reduction through natural processes (Weller 1988; Galatowitsch and van der Valk 1994; Knutsen and Euliss 2001). Such restoration would then likely restore more natural water-level dynamics within wetlands lower in the catchment and improve hydrologic processes that maintain ecological integrity of wetland systems and provide services to society (Anteau 2012). This case study also demonstrates the

importance of 1) re-evaluating previous studies that initially evaluated the condition of an ecosystem before and after a disturbance, because the full effect of the disturbance may continue beyond the temporal scale of the initial study, or 2) structuring analyses to evaluate the rate of environmental change in relation to either historical rate or to a contemporaneous rate of a complementary ecosystem process. In my case, comparing wetting and drying rates as complementary processes in wetlands within modified catchments versus unmodified catchments allowed me to evaluate long-term effects of consolidation drainage and infer the overall effect on balance of wetland water budgets.

Agricultural intensity has increased in the Prairie Pothole Region since the 1800s, generally following a southeast to northwestern pattern (Samson and Knopf 1994). As such, there has been a varying period of catchment modification (Dahl 1990). In a recent evaluation of productivity in more-permanent wetlands within the region, productivity appeared to be decreased overall and showed a spatial pattern of stronger declines in the southeast compared to the northwest (Anteau and Afton 2011). My results suggest one potential mechanism for that loss of productivity was the progressive-chronic effect of consolidation drainage, as wetlands in landscapes that have been modified for longer have had more time to reach their spill points and stabilize. In North Dakota, I found 39% of more-permanent wetlands had sufficient drainage within their catchments to unbalance their water budget and 23% of those wetlands to have filled >90% of their maximum area. The remainder of the wetlands in drained catchments likely will reach spill-over levels if management actions are not taken, but if the frequency or intensity of wetting phases increases due to climate change this process likely would be accelerated. At either rate, increased wetland size and reduced water-level fluctuation may result in a decline in productivity similar to those observed in Iowa and Minnesota (Anteau and Afton 2011).

My findings also corroborate the idea that drainage of less-permanent wetlands has led to greater amounts of water consolidated into fewer basins and those basins tend to be larger and more stable than they were historically (Krapu et al. 2004; Anteau 2012; McCauley et al. In Review). Consolidation drainage networks essentially speed the flow of surface water thereby reducing infiltration into groundwater (Winter 2003). Furthermore, more inputs into a wetland tends to reduce the surface area to volume ratio, which greatly reduces evapotranspiration (Winter 1989). Together, these mechanisms suggest that consolidation of water inhibits the natural processes that would reduce surface water within a catchment (LaBaugh et al. 1987; Winter and Rosenberry 1995; Winter 2003). Consequently, more surface water is stored in larger wetlands and when those wetlands reach spill-over levels more surface water flows out of the catchments into larger watersheds. Accordingly, consolidation drainage can convert non-contributing catchments into contributing catchments of larger watersheds, thus becoming conducive to downstream flooding.

Increased wetland size and stabilized water levels can have deleterious effects on the integrity of wetland ecosystems and the services they historically provided. As wetlands increase in size they flood new habitat that provides nutrients to drive wetland productivity through decomposition of vegetation and flooding of nutrient-rich soils. However, in modified catchments once wetland water levels reach basin spill point elevations, water levels are likely to become stabilized. Stabilization of water levels could reduce availability of nutrients in the system, because during sustained lake phases nutrients get tied up in anoxic sediments. Historically, these would become available again if the wetland draws down and sediments oxidize (Euliss et al. 1999). Stabilized water levels also might drive a change in ecological community structure because species more adapted to stable conditions become dominant where

there is a lack of water fluctuation (Van der Valk and Davis 1980). For example, *Typha* spp. proliferate in stable water environments (Swanson 1992; Shay et al. 1999; Boers and Zedler 2008); and, higher, more stable water levels allow fish populations to become established in wetlands where they were previously controlled by inhabitable conditions during drawdown periods (Peterka 1989; Anteau and Afton 2008; Herwig et al. 2010).

Prairie pothole wetlands are an important resource for migratory waterbirds during spring and fall migration and during the breeding season. Many waterbirds use these wetlands as stopover sites where they rely on invertebrates to meet energy requirements of long migration flights, and for building energy and nutrient supplies for breeding in the region or in other areas on the continent (Batt et al. 1989; Swanson and Duebbert 1989; Anteau and Afton 2006, 2011). Consequently, stabilization of water levels after chronic increases in water level is a concern for waterbird conservation because of the likely decreases in wetland productivity. Indeed, drainage of less-permanent wetlands and stabilization of water levels in more-permanent wetlands may already be affecting waterbird populations (Niemuth et al. 2006; Anteau and Afton 2011; McCauley & Anteau unpublished manuscript) and potentially other native inhabitants of these wetlands, such as amphibians (Balas et al. 2012; Herwig et al. 2013; Mushet et al. 2014).

Consolidation drainage has been implicated in water-level increases in wetlands that receive drainage water (Anteau 2012; McCauley et al. In Review), and my results suggest that past drainage causes chronic flooding effects. As more-permanent wetlands continue to increase in area, surrounding uplands are at higher risk for being flooded. Further, remaining wetlands that reach their spill point have reduced or no ability to provide flood protection and flood waters may then cascade into larger-scale watershed flooding problems. My findings suggest that once these basins fill, catchments surrounding those basins transition from a non-contributing to

contributing area of larger order watersheds. Thus, landscapes within the Prairie Pothole Region are shifting from catchments that may be only intermittently connected at the surface to larger-order watersheds with much more hydrologic connectivity. While I think it is likely this shift is occurring wherever there is consolidation drainage, there are opportunities to test this hypothesis in larger watersheds of North Dakota (e.g., Devils Lake, Red River of the North, or Missouri River) that have recently experienced flooding of increased intensity and magnitude. Using techniques such as those outlined by McCauley and Anteau (2014), more detailed study of formerly isolated catchments that are now contributing to larger watersheds could provide more accurate information regarding the impact of wetland drainage on flooding within these larger watersheds. This question deserves thorough investigation because the reduction in flood control that wetlands can provide due to consolidation drainage has probably had a great economic cost, and those costs will continue to come in the form of inundated property, damaged infrastructure, and new flood control infrastructure lower in the watershed.

Progressive-chronic effects of anthropogenic modifications to the environment are likely present throughout other systems. For example, installation of dams on river systems likely has a static-chronic effect on flows if water management is consistent, but those dams may have a progressive-chronic effect on sediment accumulation in reservoirs and river-bed incision. Anthropogenically induced environmental change continues to alter services that ecosystems provide to society, while reducing the integrity of the ecosystem, which likely will result in permanent ecosystem change. There is a fundamental difference between managing the cumulative harmful effects of continued anthropogenic disturbance to ecosystems, and identifying and managing legacy effects of past disturbances that continue to degrade ecosystems. Fortunately, identifying the positive feedback mechanisms within ecosystems that

were initiated by historical disturbances could help land managers improve their ability to develop management strategies to counteract these disturbances on managed ecosystems.

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CHAPTER 3. IS CONSOLIDATION DRAINAGE AN INDIRECT MECHANISM FOR INCREASED ABUNDANCE OF CATTAIL IN NORTHERN PRAIRIE WETLANDS?

Abstract

Plant communities are structured by environmental conditions and the variability in those conditions. Within northern prairie wetlands these conditions are primarily driven by water levels and water chemistry. Therefore, disturbances to wetlands or their catchments that disrupt water-level fluctuations in response to wet–dry climatic periods have the potential to alter natural vegetative communities in favor of species that proliferate in stable environments, such as cattail (*Typha* spp.). I evaluated the effect of water-level dynamics during a recent wet–dry climate fluctuation on cattail coverage within wetlands situated in catchments with varying land use and amounts of wetland drainage. I found that water depth increased more where wetlands filled less of their topographic basin ($\hat{\beta}$ = -0.006 ± 0.002 SE), had steeper bank slopes ($\hat{\beta}$ = 0.124 ± 0.042 SE), and were in larger catchments ($\hat{\beta}$ = 0.069 ± 0.032 SE). Proportion of the wetland covered by cattail was negatively correlated with increased water depth ($\hat{\beta}$ = -0.090 ± 0.027 SE), bank slope ($\hat{\beta}$ = -0.067 ± 0.013 SE) and wetland area ($\hat{\beta}$ = -0.039 ± 0.013 SE). Existing evidence suggests that drainage of wetlands within catchments of remaining wetlands causes water levels to progressively increase until the topographic basin fills and then water levels stabilize. Thus, the eventual filling and stabilizing of wetlands caused by consolidation drainage offers a potential mechanism for increased cattail coverage observed on the northern prairie landscape. Increased cattail coverage within a wetland reduces the quality of the wetland to support diverse plant, invertebrate, and waterbird communities.

Introduction

It has been suggested that the prevalence of monotypic stands of cattail (*Typha* spp.) has increased for prairie wetlands (Kantrud 1992; Swanson 1992; Anteau and Afton 2008), which has implications for abundance and quality of food resources and foraging habitat for waterbirds, particularly shorebirds. When shallow-water zones become dominated by cattails, wetlands have less shallow-water foraging habitat, a reduction in or absence of submerged aquatic vegetation, and a reduction in the variety of decomposer organisms—including macroinvertebrates that are important food resources for waterbirds (Voigts 1976; Kantrud 1986). Monotypic stands of cattails within wetlands may eliminate foraging and roosting habitat needed by migrating and breeding shorebirds and waterfowl (Weller and Spatcher 1965; Voigts 1976; Kantrud 1986; Anteau 2012). Landscape modifications likely have altered natural wetland hydrology that included water-level fluctuation, changed sedimentation and nutrification, or introduced species within wetlands (Galatowitsch et al. 2000; Gleason et al. 2003; Anteau 2012). Such changes might be responsible for greater cattail abundance and resultant degradation of many wetland ecosystems across North America (Galatowitsch et al. 1999). Therefore, it is important to understand how landscape modifications have influenced the abundance of cattails and the concomitant value of those wetlands to waterbirds to inform ongoing conservation efforts to reverse the trend of increasing cattail encroachment in wetlands of the Prairie Pothole Region.

Hydrologic fluctuations in response to climate variability help shape floral community structure of prairie wetlands. While plant community composition shifts in response to wet–dry climate periods, the overall community structure is dominated by floral species adapted to dynamic hydrologic conditions (Stewart and Kantrud 1972; Grace and Wetzel 1981; LaBaugh et al. 1987; Kantrud et al. 1989; van der Valk 2005). Higher and more-stable water regimes may

shift emergent communities toward cattail-dominated systems because cattails proliferate in more-stable environments (Swanson 1992; Shay et al. 1999; Boers and Zedler 2008).

Disturbances within wetlands and their surrounding catchment that increase sedimentation and nutrient loading into wetlands or stabilize water levels may create conditions more favorable to cattail invasions in prairie pothole wetlands (Wang et al. 1994; Gleason and Euliss 1998; Shay et al. 1999). Increased sedimentation can decrease wetland depth through addition of nutrient-rich soil while reducing or eliminating competing wetland plant species (Jurik et al. 1994; Gleason and Euliss 1998). These conditions favor development of monotypic stands of cattail (Gleason and Euliss 1998; Galatowitsch et al. 1999; Shay et al. 1999). Further, additional nitrogen inputs from uplands can promote growth and expansion of cattail, especially where nitrogen is limiting (Shay et al. 1999). Moreover, stabilization of water levels can increase soil release of phosphorus and increase uptake by cattail resulting in enhanced growth (Boers and Zedler 2008). Nutrient enrichment of wetlands with high and stable water-levels can lead to changes in vegetation structure and consequently changes in the macroinvertebrate community (Voigts 1976; McCormick et al. 2004) because species that are best adapted to exploit available nutrients will gain a competitive advantage over those adapted for a more oligotrophic environment.

In the Prairie Pothole Region of North Dakota, cattail was previously found during 2002 to be present in 28% of wetlands and averaged 37% areal coverage within wetlands that contained cattail (Ralston et al. 2007). It is likely that monotypic stands of cattail will continue to increase in occurrence and coverage within wetlands where hydrology has been modified and uplands disturbed (Kantrud 1992; Swanson 1992; Anteau and Afton 2008); therefore, there is a need to quantitatively evaluate factors that may be contributing to wetland conditions that are

favorable to increased cattail coverage. Accordingly, I examined the influence of hydrologic and land-use factors on coverage of cattail within semipermanent and permanent wetlands. I expected cattail coverage to be greater within wetlands where water levels were more stable and where agricultural land-use modified uplands with drainage networks and tillage.

Methods

Study Area

I returned to wetlands within the Prairie Pothole Region of North Dakota (Figure 3.1) that were previously randomly selected and surveyed once in 2004 or 2005 (hereafter, 2004/05) by Anteau and Afton (2008; n = 153). Wetlands were randomly selected within a hierarchal sampling design of three regions, three sub-regions, clusters of three townships, and three wetlands within each township (Anteau and Afton 2008). Accordingly, I included township as a random error term to account for this clustered design. These were lacustrine semipermanent and shallow-water permanent wetlands (Cowardin et al. 1979) that must have had an open-water area larger than 120 m across to be surveyed in 2004/05. In 2004/05, if reselection in the field was necessary, the nearest suitable semipermanent wetland was surveyed. In April and May of 2011, I returned to 126 of the original 153 wetlands. Based on the National Wetland Inventory classification (NWI; U.S. Fish and Wildlife Service 2003), 67% of wetlands surveyed were semipermanent, 3% seasonal, and the rest were permanent wetlands or shallow-water lakes. Those wetlands classified by NWI as seasonal were wetlands reselected in the field in 2004/05 that were more characteristic of semipermanent wetlands at time of field assessment.

My selection of wetlands was not completely random in regards to cattail coverage within semipermanent and permanent wetlands throughout the region. My selection was confined to more-permanent wetlands that had at least 120 m of open water to address objectives

of another study (Anteau and Afton 2008). Therefore, my observations under represent cattail coverage across the region and should not be used for such estimation. However, my data set should provide a good basis for understanding cattail dynamics with the exception of not containing information for completely choked wetlands.

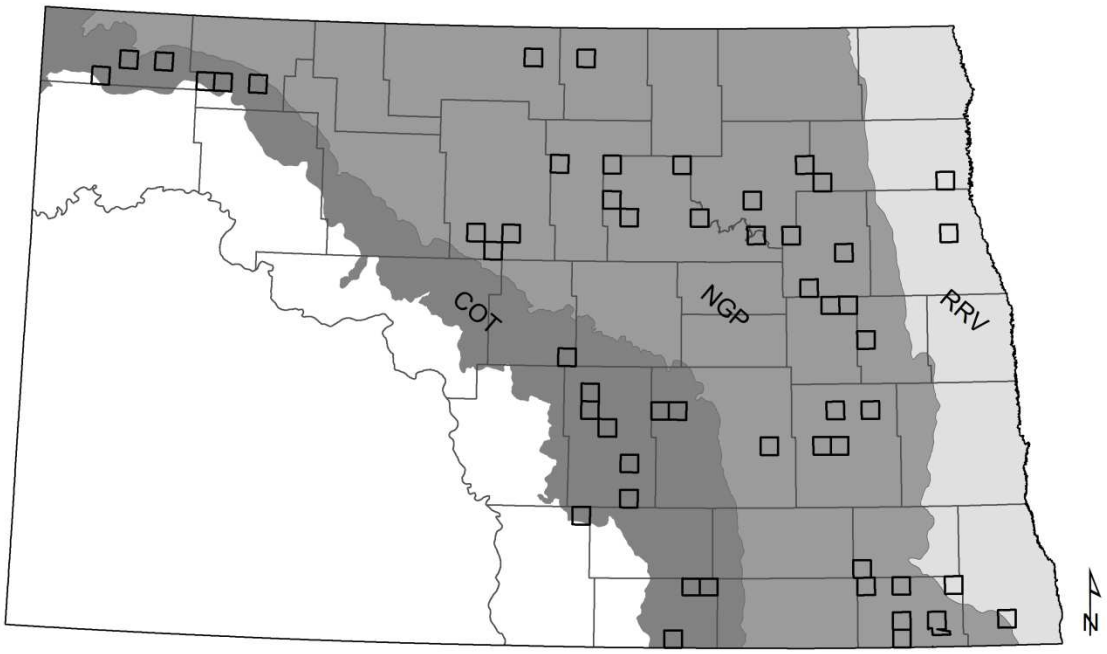

Figure 3.1. North Dakota study area showing townships where wetlands were surveyed during early spring of 2004, 2005, 2010 and 2011. Shaded areas are three physiographic regions of the Prairie Pothole Region: Red River Valley (RRV), Northern Glaciated Plains (NGP), and Missouri Coteau (COT).

Spring Wetland Surveys and Data Preparation

Water depth

To estimate change in depth among surveys of 2004/05 (Anteau and Afton 2008) and surveys of 2011, I measured water depth (± 0.1 m) at 10 locations estimated to be 10 m into open water from either the shoreline or emergent vegetation to open-water interface for 2004/05.

When waves were present, I recorded the average depth between wave crests and troughs. Prior to field work, I delineated the shoreline or emergent vegetation to open-water interface of each wetland using imagery (National Agricultural Imagery Program, U.S. Department of Agriculture; hereafter NAIP) acquired in the summer (July) prior to each spring survey conducted by Anteau and Afton (2008). I used the imagery from the previous year because it better represents the location of the emergent vegetation to open-water interface that Anteau and Afton (2008) used to locate their sampling locations. I digitized the interface by using a geographic information system (GIS) at a scale of 1:5,000. I offset (i.e. buffered) the digitized open-water interface by 10 m in the direction of the wetland center to approximate locations of 2004/05 sampling. I derived my 10 random points from the 10-m buffer, but I constrained point locations so there is a minimum distance of 40 m between points. I navigated to survey locations that were pre-loaded onto a GIS data logger (Trimble GeoXT, Trimble Navigation, Sunnyvale, CA). Survey locations found within the emergent vegetation ring were recorded as such, because different dynamics of sedimentation and accumulation of organics were expected.

Emergent vegetation

I estimated the width of emergent vegetation coverage (0, 1–4, 5–10, 11–30, 31–60, or >60 m) and the proportion (± 0.1) of emergent vegetation that was cattail at 10 randomly selected transects that extended perpendicular from the shoreline through the random points where water depth measurements were taken to the center of the wetland. I calculated an average width of cattail coverage for each wetland using the midpoint value of the 10 categorical estimates of emergent vegetation coverage (maximum value of 90 m) multiplied by the proportion that was cattail. Finally, I calculated the area of cattail coverage within each wetland

by using a GIS to create a polygon from the perimeter of the wetland measured using 2010 imagery (see below) extending inward the distance of the average width of cattail coverage.

Land use

I classified current agricultural impacts immediately surrounding each wetland using ground observations in 2011. I used GIS software in the field to attributed empty polygon outlines of land-cover data (Habitat and Population Evaluation Team 1996) based on current observations with one of the following categories: native grassland, restored grassland, unknown grassland, hayland, cropland, shrubs, trees, developed, barren, or wetland. I calculated the proportion of cropland for the upland area that was both within the defined catchment (see below) and within 400 m of the subject wetland. I also estimated the width of upland grass buffer (0, 1-4, 5-10, 11-50, >50 m) between any development or agricultural land use and the wetland. In my analyses I used the midpoint of categorical estimates, with maximum value of 75 m.

Water surface area

I used water surface area delineated for each surveyed wetland by McCauley et al. (In Review) using photointerpretation of NAIP aerial imagery for 2003–2006 and 2009–2010. Photointerpretation was performed while images were viewed as panchromatic instead of true-color, because they were done as part of a larger study that involved some panchromatic imagery (see McCauley et al. In Review). Where the waterline was obscured by emergent vegetation, the waterline was approximated to be halfway between the emergent-vegetation to open-water interface and clearly identifiable upland. NAIP imagery was not available for 2007 and 2008. For those years I used wetland water surface area delineated once in either 2007 or 2008 using high-resolution digital elevation model (DEM; source data: 1 m pixel lidar; Data available from

the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR) orthorectified image (Intermap Technologies, Inc., Englewood, Colorado).

Catchments

I used wetland catchments as an index of watershed derived wetland complexes defined as the portion of the landscape in which surface water flows into a focal wetland, and included more-intermittent wetlands and their catchments (McCauley and Anteau 2014; McCauley et al. In Review). Catchments were derived for each of the surveyed wetlands using high resolution DEMs (3 m pixel lidar or 5 m pixel IfSAR) and surface hydrology modeling tools (McCauley and Anteau 2014; McCauley et al. In Review). Some catchments (46%) that were large or highly irregular in shape were truncated to a 2.5 km maximum radius from the wetland basin for logistical reasons associated with assembling landscape variables, such as amount of wetland area drained. The 2.5-km radius encompassed >90% of the total catchment area for 68% of catchments. Landscape conditions within these 2.5-km truncated catchments should represent the condition of the full catchment, and the conditions nearest the wetland basin likely influence the basin most. Therefore, I assumed the 2.5-km-truncated catchment provided a reasonable area to evaluate impacts of land use in our system and are an improvement over the simply buffering around a wetland a set distance, a common practice (McCauley and Anteau 2014).

Catchment drainage

I used estimates of the percent catchment area that was drained wetland during 2003–2010 using multiple data sources, including: aerial photographs, DEM, NWI, and spatially explicit soil data (McCauley et al. In Review). Wetlands were identified as drained if they were present in historical photographs (dating back to 1937) but not present in current photographs, or if the wetlands were identified as part of a drainage network. Significant drainage occurred prior

to 2003 in our study area; however, there was negligible evidence of additional drainage after 2003.

I also recorded presence of drainage networks and connections between wetlands while in the field in 2011. Surface-water connections include: inflow and outflow streams, ditches, culverts, and temporal connections between wetland basins.

Basin area

I defined a wetland basin as the topographic depression that collects surface water that which is isolated from basins of other wetlands of an equal or more permanent hydroperiod. I measured the basin area to determine the maximum water surface area of a wetland that the basin could hold before the water would spill and flow out of the basin. I used the high-resolution DEMs (3 m pixel lidar or 5 m pixel IfSAR) to find the spill point of the basin and then delineated the area at that spill point elevation within the basin. Because wetlands in basins that were near full or that were full would have less surface area dynamics (Chapter 2), I calculated the proportion of the basin that the focal wetland filled at the start of each climate phase.

Climate

I used a fine-scale climate index (2.5 arc-minute) derived by Post van der Burg et al. (In Prep.) to estimate the spatially-explicit effect of climate on increase in water depth of wetlands. The climate index used a standardized precipitation-evapotranspiration index calculated from PRISM (Parameter-elevation Regression on Independent Slopes Model) Climate Group data (PRISM Climate Group 2002). The temporal summary of the index that best explained water levels in the current era, and used here, incorporated climate conditions over the previous six years with a uniform average across years (Post van der Burg et al. In Prep.). For each wetland, I

calculated the difference in climate index values from the wet period during 2003–2005 and wet period in 2009–2010.

Statistical Analyses

Water depth increase

I examined the potential influence of climate, upland disturbance and wetland connectivity on increased in wetland depth from 2004/05 to 2011 using mixed-effects regression analysis (Package *lme4* in R Statistical Computing Environment; R Development Core Team 2010; Bates et al. 2011). I created an *a priori* full model that included independent variables including: difference in climate index, percent catchment area that was drained wetland, presence/absence of wetland surface connections, percent surrounding upland that was cropland, basin full percent, natural logarithm of bank slope, and natural logarithm of catchment area. I also included interaction terms for difference in climate index-by-catchment area because climate variability likely has a greater influence on water depth of wetlands in smaller catchments than on larger catchments, and for wetland drainage-by-basin full percent because water depth within wetlands that already filled their basins would be less influenced by drainage within the catchment than would wetlands that have potential for increased water depth. I found no evidence of strong correlations among dependent variables within the full model ($|r| \leq 0.24$).

I evaluated variables in my *a priori* full model by comparing a one-variable-removed reduced model to the full model (Arnold 2010). I assumed the removed variable was informative if the Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson 2002) of the reduced model was increased ≥2 points; all informative variables were compiled into a final reduced model. I first evaluated each two-way interaction relative to the full model and removed any interactions not supported from the full model before conducting the

variable selection process for all main effect variables. I specified township as a random error term. I compared the final model to a null model using AIC_C to determine model adequacy (Burnham and Anderson 2002). I evaluated the variation captured by the model from interpretation of the squared correlation coefficient from the observed and fitted values.

Cattail coverage

I evaluated how coverage of cattail within wetlands in 2011 may have been influenced by the change in water depth from 2004/05 to 2011, rate of water surface area change during a drying phase 2003–2005 to 2006–2008, wetland drainage within the catchment, and amount of upland that is cropland using a mixed effect regression analysis (Package *lme4* in R Statistical Computing Environment; R Development Core Team 2010; Bates et al. 2011). In my *a priori* full model I also included the natural logarithm of wetland area, percent of the topographic basin filled by the wetland, natural logarithm of bank slope as independent variables, and I included a cropland-by-upland buffer width interaction term because a grass upland buffer can mitigate the effects of surrounding land use on wetland quality (Anteau and Afton 2008; Anteau et al. 2011). I found no evidence of strong correlations among independent variables within the *a priori* full model ($|r| \leq 0.25$), with the exception of cropland and upland buffer ($r = -0.65$) for which the interaction term was included. I evaluated independent variables in the full model and created a reduced model using the variable selection method described above. I specified township as a random error term, compared the final model to a null model using AIC_C to determine model adequacy (Burnham and Anderson 2002), and evaluated the variation captured by the model from the squared correlation coefficient of the observed and fitted values. I plotted model predicted effects across the observed range of variable of interest and held other variables at median levels. I used 85% confidence intervals for interpretation of importance for variables to

be more consistent with the threshold used during variable selection within the full model using AIC_C (Arnold 2010).

Results

Within the 126 wetlands visited in early spring of 2011 average water surface area was 68 ha (median = 26 ha, range = 1–965 ha, SD = 132) in July of 2010. Maximum water depth within wetlands in spring 2011 averaged 2.0 m (SD = 0.7), and on average, wetland water depth increased 1.1 m (SE = 0.1) from 2004/05 to 2011 (Figure 3.2). We detected cattail on at least one transect at 51% of wetlands.

My final model used to explain increased water depth contained independent variables including: percent basin full, bank slope, catchment area, and difference in climate index (Table 3.1). This model explained 54% of the variation in water depth increase and was 16 AIC_C points better than a null model and held all of the Akaike model selection weight (w_i). Water depth increased more where wetlands filled less of their topographic basin, had steeper bank slopes, and were in larger catchments (Table 3.2). Increase in wetland depth also occurred where climate index indicated wetter conditions (Table 3.2).

My final model used to explain cattail coverage within wetlands contained independent variables including: increase in water depth, bank slope, and wetland area (Table 3.3). This model explained 38% of the variation in cattail coverage among wetlands and was better than a null model ($\Delta AIC_C = 43$, $w_i = 0$). Proportion of wetlands covered by cattail was negatively correlated with increased water depth ($\hat{\beta} = -0.090 \pm 0.027$ SE; Figure 3.3). Cattail coverage was also negatively correlated with bank slope ($\hat{\beta} = -0.067 \pm 0.013$ SE) and wetland area ($\hat{\beta} = -0.039 \pm 0.013$ SE).

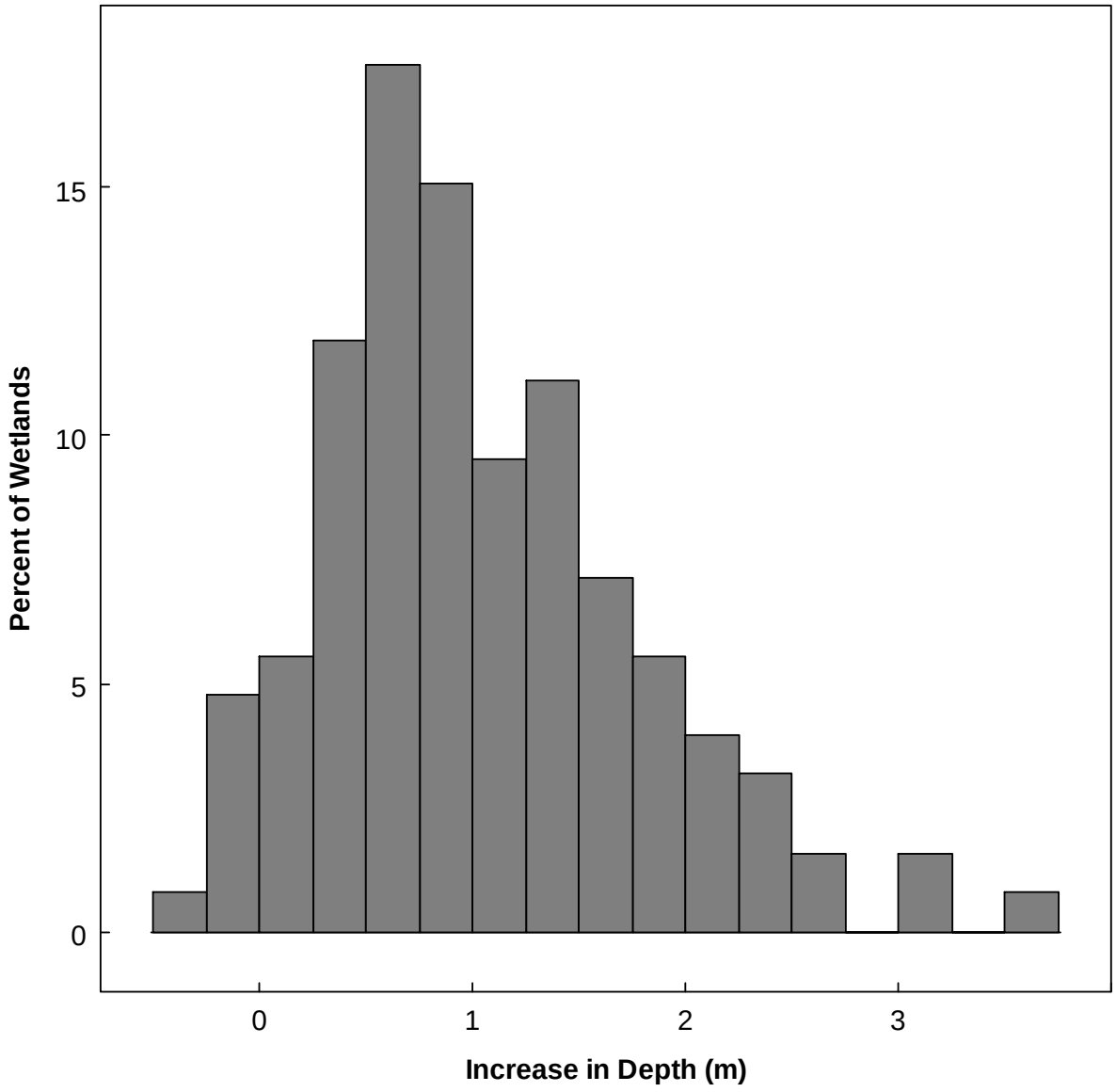

Figure 3.2. Histogram showing increased water depth within 126 more-permanent wetlands in North Dakota from 2004 or 2005 to 2011.

Table 3.1. Reduction of independent variables from an *a priori* full model used to examine the effect of wetland setting and climate on water depth increase in more-permanent wetlands from 2004 or 2005 to 2011 in North Dakota. Changes in model log likelihood (ΔLL), number of estimated parameters (ΔK), and Akaike's Information Criterion for small sample size (ΔAIC_C) are reported for the model with that variable removed relative to the referenced full model. We deemed covariates important (IMP) if their removal causes a >2 ΔK increase in AIC_C. A colon indicates an interaction between variables.

Variable Removed	ΔLL	ΔK	ΔAIC_c	IMP
Climate : Catchment Area [a]	-0.9	-1	-0.6	No
Drainage : Basin-Full [a]	-0.1	-1	-2.2	No
Basin-Full [b]	-4.1	-1	5.8	Yes
Bank Slope [b]	-3.5	-1	4.7	Yes
Climate [b]	-3.3	-1	4.3	Yes
Catchment Area [b]	-2.4	-1	2.4	Yes
Cropland [b]	-0.4	-1	-1.5	No
Surface Connection [b]	-0.2	-1	-2.0	No
Drainage [b]	0.0	-1	-2.4	No

[a] Compared to full model: LL = -122.2, K = 12, AIC_C = 271.2
[b] Compared to model with no interactions: LL = -123.2, K = 10, AIC_C = 268.3

Table 3.2. Estimated coefficients ($\hat{\beta}$), standard errors (SE), and 85% lower (LCL) and upper (UCL) confidence limits for fixed effects within the final reduced model used to examine the effect of wetland setting and climate on water depth increase in more-permanent wetlands from 2004 or 2005 to 2011 in North Dakota.

Fixed Effects	$\hat{\beta}$	SE	LCL	UCL
Intercept	1.4544	0.3046	1.0159	1.8930
Basin-Filled	-0.0063	0.0022	-0.0094	-0.0032
Bank Slope	0.1243	0.0419	0.0640	0.1847
Catchment Area	0.0687	0.0315	0.0233	0.1140
Climate	0.3062	0.1234	0.1285	0.4839

Table 3.3. Reduction of independent variables from an *a priori* full model used to examine the effect of hydrology and wetland setting on coverage by cattail within more-permanent wetlands in North Dakota in 2011. Changes in model log likelihood (ΔLL), number of estimated parameters (ΔK), and Akaike's Information Criterion for small sample size (ΔAIC_C) are reported for the model with that variable removed relative to the referenced full model. Covariates were deemed important (IMP) if their removal causes a >2 ΔK increase in AIC_C.

Variable Removed [a]	ΔLL	ΔK	ΔAIC_c	IMP
Bank Slope	-10.1	-1	17.8	Yes
Depth Change	-6.2	-1	9.9	Yes
Wetland Size	-3.9	-1	5.4	Yes
Drying Rate	-1.0	-1	-0.4	No
Basin-Full	-0.8	-1	-0.8	No
Drainage	-0.2	-1	-2.1	No
Cropland [b]	-0.5	-2	-3.8	No
Upland Buffer [b]	-0.4	-2	-4.0	No

[a] Compared to full model: LL = -122.2, K = 12, AIC_C = 271.2
[b] Required also removing the interaction of Cropland-by-Upland Buffer

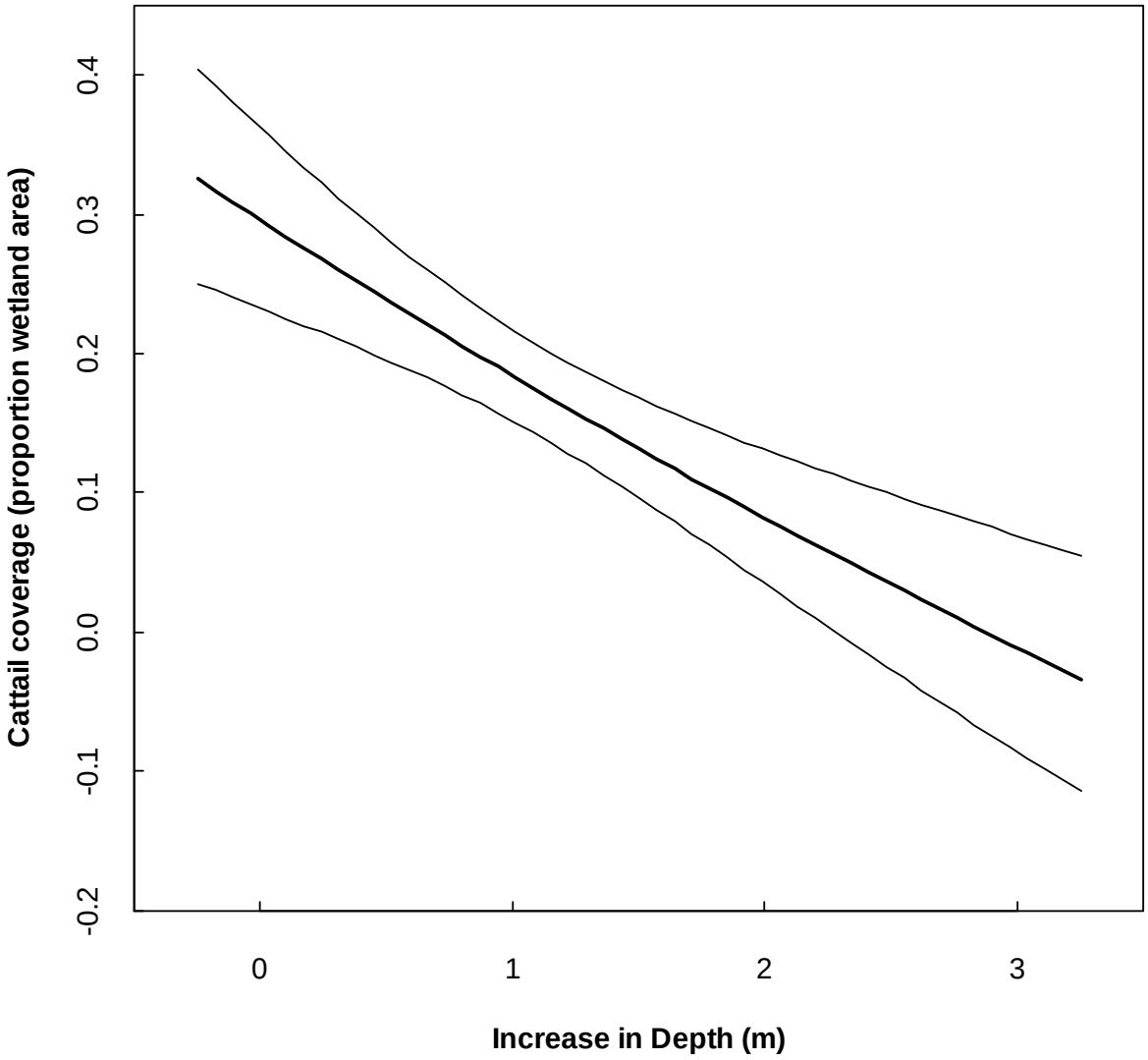

Figure 3.3. Model estimated effect (85% CI) of increase in water depth on cattail coverage within more-permanent wetlands in North Dakota.

Discussion

My results show that wetland water depth was greater during the recent wetting phase than that at the end of the previous wet period. However, increases in water depth were limited within wetlands that had already filled, or nearly filled to their topographic basin. Additionally, I observed a strong correlation between increased water depth and less cattail coverage, suggesting

cattail was eliminated where water depth increased. This process of cattail elimination by flooding during wet periods is consistent with observations from other studies (Weller and Spatcher 1965; van der Valk 1994). When combined with evidence that drainage of wetlands within catchments of remaining wetlands causes water levels to progressively increase with each wet–dry climate period until wetlands fill their topographic basin and then water levels stabilize (Chapter 2), cattail coverage is kept in check by increases in water level resulting from consolidation drainage, but ultimately will increase once water levels stabilize at their basin spill elevation.

Cattail seed germination during drawdown and growth during re-flooding is part of the natural vegetative cycle in prairie pothole wetlands (Weller and Spatcher 1965; van der Valk and Davis 1978). Wetlands that experience flooding and drawdown of equal amplitude should exhibit these natural vegetative cycles. However, when hydrologic responses to climate variability are disrupted by disturbances within the wetland systems, then vegetative cycles are also likely to be disrupted resulting in monotypic stands of cattail (Van der Valk and Davis 1980). For example, where consolidation drainage has resulted in higher and more-stable water levels in remaining wetlands, cattail can become established at the fringes of high water levels. Cattail is not likely to be eliminated by flooding within wetlands that have filled their topographic basin because these wetlands have reached their spill-point at which they contribute to larger watersheds with additional inflow. However, expansion of cattail toward the center of the wetland can occur by extension of the habitable zone as a result of sedimentation and accretion of organic debris (Waters and Shay 1992; Gleason and Euliss 1998; Shay et al. 1999). Accumulation of sediment and organic debris increases the rate of habitable zone expansion, ultimately reducing the water depth required to reach the basin spill point elevation. Wetlands in

landscapes with high agricultural land use are likely to have greater rates of sedimentation and nutrient input (Gleason and Euliss 1998), than those surrounded by grasslands, making those wetlands prime environments for cattail.

Consolidation drainage appears to have more of an indirect effect on increased cattail coverage in wetlands through altered water-level fluctuations, rather than a direct effect. Consolidation drainage actually could keep cattail coverage low in wetlands that have not yet filled their topographic basin, because as a result of each climatic wetting phase water levels progressively increase (Chapter 2) to flood existing cattail stands. However, that is only a temporary response, until a wetland basin is full and water levels stabilize. Once water-levels stabilized, cattail coverage is likely to increase within wetlands where consolidation drainage has occurred.

My observations provide evidence that landscape modifications that have altered hydrologic processes within wetlands have the potential to alter natural vegetative cycles, resulting in increased coverage of cattail in monotypic stands rather than more diverse plant communities interspersed within wetlands. This change can negatively impact invertebrate forage and waterbird populations that feed on aquatic invertebrates. Restoration of more natural water-level fluctuations in response to wet–dry climate periods, perhaps through restoration of complexes of wetlands with vary hydroperiods, may restore vegetative cycles and transition monotypic stands of cattail back into vegetative communities that vary in wetland coverage according to hydrologic conditions.

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CHAPTER 4. ALTERED WETLAND HYDROLOGY SUPPORTS INCREASED PRESENCE OF FISH IN PRAIRIE POTHOLE WETLANDS ACROSS NORTH DAKOTA

Abstract

In prairie wetlands fish have been implicated in the degradation of habitat for aquatic invertebrates and in turn for waterbirds. Historically, fish occurrence had been mostly low, approximately 10–20%, and intermittent in semipermanent and permanent wetlands within the Prairie Pothole Region due to their depth, chemical and hydrological dynamics, and isolation. However, landscape modifications such as consolidation drainage of wetlands have increased water levels, connectivity, and hydroperiods of remaining wetlands. I evaluated how these changes have influenced the occurrence and abundance of fish in prairie wetlands of North Dakota and how fish have influenced wetland quality, as measured by the amount of submerged aquatic vegetation, turbidity, and the nature of aquatic invertebrate communities. Fish were present in 57% of 138 semipermanent and permeant wetlands surveyed in 2011, an increase of 14% compared to surveys conducted in 2004 and 2005. Logistic regression analysis indicated a higher probability of fish occurrence in wetlands that had greater water depth ($\hat{\beta}$ = 0.625 ±0.319 SE) and greater wetland connectivity by means of more full topographic basins ($\hat{\beta}$ = 0.020 ±0.009 SE). Fish abundance was similarly related to water depth ($\hat{\beta}$ = 0.231 ±0.082 SE) and more full topographic basins ($\hat{\beta}$ = 0.007 ±0.002 SE), indicated by mixed-effect regression analysis. Fathead minnow abundance was positively correlated with turbidity ($\hat{\beta}$ = 2.735 ±0.709 SE) and negatively correlated with abundance of submerged aquatic vegetation ($\hat{\beta}$ = -0.209 ±0.088 SE) and invertebrate biomass ($\hat{\beta}$ = -0.097 ±0.041 SE) in multivariate multiple regression analysis. These results indicate an indirect negative influence of consolidation drainage on

wetlands' ability to support productive and diverse invertebrate communities and the waterbird populations that rely on them, through increased fish abundance and turbidity and decreased abundance of submerged vegetation.

Introduction

Distribution of fish in wetlands in the Prairie Pothole Region is influenced by isolation of wetland basins, water depth, and water chemistry all of which are dynamic as a result of fluctuations between wet and dry climate periods (LaBaugh et al. 1987; Kantrud et al. 1989; Peterka 1989; Euliss et al. 1999; Leibowitz and Vining 2003). However, anthropogenic modifications to prairie landscapes have been linked to disruptions of water-level fluctuations and basin isolation (Euliss and Mushet 1996; Merkey 2006; Anteau 2012). Specifically, consolidation drainage of wetlands in prairie landscapes has led to more-permanent, larger wetlands that contain more surface connections to other wetlands (McCauley et al. In Review; Chapter 2). As a result, these modifications may contribute to an increase in the distribution and abundance of fish in wetlands (Zimmer et al. 2000; Anteau 2012).

Fish populations in most semipermanent prairie wetlands historically have been intermittent, dependent upon how wet or dry wetlands are in response to climate fluctuations (Kantrud et al. 1989; Peterka 1989). During wet periods, fish disperse through flooded connections among semipermanent and permanent wetlands (Kantrud et al. 1989). Flooding of previously dried areas within these wetlands induces a pulse in invertebrate productivity providing abundant food that facilitates growth of local fish populations (Euliss et al. 1999; Hanson et al. 2005). Higher water-levels provide areas of wetlands that are deep enough for over-winter survival or provide connections to other areas of winter refugia (Zimmer et al. 2001a). However, when water levels recede wetlands become isolated and fish are less likely to

survive as hypoxic conditions cause a winterkill or summerkill event (Kantrud et al. 1989; Peterka 1989).

Changes in wetland hydrology have the potential to influence ecological communities in prairie wetlands because native communities are the result of a dynamic and surface isolated system. Higher, more stable water regimes may shift species composition toward a community with species that are adapted to more stable environments. Further, increased connectivity among basins would provide colonization corridors and deep-water refugia for fish that rarely colonized isolated basins (Herwig et al. 2010). Together these conditions are more favorable for fish that were previously kept in check by hydrologic dynamics and geographic isolation of wetlands to become invasive and further threaten natural functions of prairie wetlands (Scheffer et al. 1993; Hanson et al. 2005; Herwig et al. 2010; Anteau et al. 2011).

Compared to historical accounts, the prevalence of fish in prairie wetlands was apparently increased in 2004 and 2005, during a high-stable-water regime (Anteau and Afton 2008; Anteau et al. 2011). Increases in occurrence and abundance of fish can decrease abundance of invertebrates in wetlands thereby reducing forage quality and foraging efficiency for waterbirds (Swanson and Nelson 1970; Cox et al. 1998; Hanson et al. 2005; Anteau and Afton 2009). High abundance of fish can impact density of macroinvertebrates (e.g., amphipods and cladocerans) in wetlands directly through predation and indirectly through increased turbidity, which decreases submerged vegetation habitat for invertebrates, both resulting in a change in wetland trophic structure (Scheffer et al. 1993; Hanson and Butler 1994; Zimmer et al. 2000; Zimmer et al. 2001b; Anteau et al. 2011). Abundance of fathead minnows (*Pimephales promelas*) are of particular interest regarding the quality of a wetland to support waterbirds in the region because they are tolerant of a wide range of environmental conditions, have a high rate of

reproduction, and are large enough to eat macroinvertebrates, yet have also been found to feed on detritus that may increase turbidity (Held and Peterka 1974; Gale and Buynak 1982; Hanson and Riggs 1995; Duffy 1998; Herwig and Zimmer 2007).

Here I examined how landscape modifications that have been linked to higher water levels, altered water-level fluctuations, and increased wetland connectedness (McCauley et al. In Review; Chapter 2) have influenced occurrence and abundance of fish in semipermanent and permanent prairie wetlands of North Dakota. I evaluated their influence on occurrence of fish in 2011, with the expectation that fish had a higher probability of occurrence in wetlands within modified catchments where water depths were greater and wetlands were more connected based on evidence from previous studies (Herwig et al. 2010; Anteau et al. 2011; Maurer et al. 2014). Further, I evaluated whether these factors also increased abundance of fish. Lastly, I evaluated whether abundance of fish had a negative influence on wetland quality measured by the amount of submerged aquatic vegetation, turbidity, and invertebrate densities and biomass (Hanson and Butler 1994; Anteau et al. 2011; Maurer et al. 2014). Through these evaluations, I evaluate the direct effect landscape modifications have on increased fish occurrence and abundance in wetlands and indirect effect landscape modifications have on wetland community structure and productivity through altered wetland hydrology and increased fish abundance.

Methods

Study Area

In 2011, I returned to 138 wetlands within the Prairie Pothole Region of North Dakota (Figure 4.1) that were previously randomly selected and surveyed once in 2004 or 2005 (hereafter, 2004/05) by Anteau and Afton (2008). These were lacustrine semipermanent and shallow-water permanent wetlands (Cowardin et al. 1979) that must have had an open-water area

larger than 120 m across to be included in the sample during 2004/05. In 2004/05, if reselection in the field was necessary, the nearest suitable semipermanent wetland was surveyed. In 2011, I returned to the 81 original wetlands and surveyed 57 additional randomly selected wetlands. Based on National Wetland Inventory classification (NWI; U.S. Fish and Wildlife Service 2003), 93 of wetlands were semipermanent, 5 seasonal, and 40 permanent wetlands or shallow-water lakes. The wetlands classified by NWI as seasonal were included because they were more characteristic of a semipermanent wetland at time of field assessment.

Spring Wetland Surveys

In April and May of 2011, I surveyed wetlands using techniques described in Anteau and Afton (2008) to collect data on fish abundance, invertebrate density, water quality, and wetland vegetation structure. I collected data on randomly located transects extending from shoreline toward the center of the wetland. I recorded data electronically and georeferenced all sampling locations at the time of collection with a geographic information system (GIS) data logger (Trimble GeoXT, Trimble Navigation, Sunnyvale, CA).

Fish communities

I used minnow traps and an experimental gill net in wetlands to determine relative abundance of fish (Anteau and Afton 2008). I set five Gee-style minnow traps with 6.35-mm mesh at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation is present) at five transects. I set the monofilament experimental gill net (21 × 2 m with seven 3-m panels ranging in mesh size from 1.9–7.6 cm) at one of the five transects, positioned perpendicular to the shoreline with the small mesh end of the net at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation was present). Minnow traps and the gill net were deployed for 12–24

hours including an overnight period. At the time of trap and gill net retrieval, I sorted and counted fish by species and by length category (<5, 5–10, 10–20, 20–40, >40 cm).

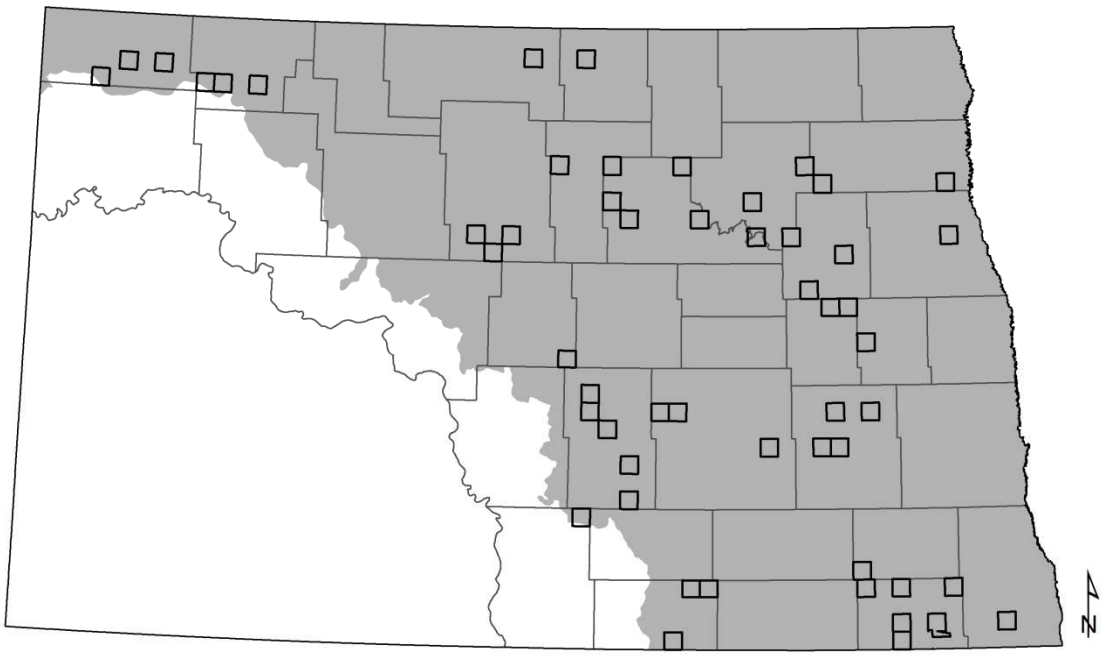

Figure 4.1. North Dakota study area showing townships where wetlands were surveyed during early spring of 2004, 2005, and 2011. Counties are outlined within the shaded region representing the Prairie Pothole Region.

I classified fish captures into one of three categories: fathead minnows, other small fish species typically <10 cm (e.g., other minnows [Cyprinidae], darters [Anhingidae], and sticklebacks [Gasterosteidae]), and large fish species typically >10 cm (e.g. northern pike [*Esox lucius*], walleye [*Sander vitreus*], yellow perch [*Perca flavescens*], sunfishes [*Lepomis* spp.], and bullhead and catfish [Ictaluridae]). I calculated catch per unit effort (relative abundance) for each gear type by dividing the number of captures of each class by the hours the gear was in the water. For each class, I summed the quotients of the two gear types. I also calculated catch per unit effort for all three fish classes combined.

Invertebrate densities and biomass

I surveyed invertebrates in open water using a D-shaped sweep net (1,200 µm mesh, 0.072 m^2 opening, WARD'S Natural Science, Rochester, NY) at the four of five transects used for minnow traps; I excluded the one used for the gill net. Sampling stations at each transect were located at 10 and 60 m from the shoreline or emergent vegetation to open-water interface. Survey locations were adjusted along transects to ensure the station depth was between 0.5 and 3 m (see Anteau and Afton 2008). I recorded depth at each sampling station to the nearest 0.1 m. At each station, a sweep-net sample consisted of a sweep across the bottom for a distance equal to the water depth, and a sweep up through the water column. I calculated the volume of water surveyed (VS; m^3) with a sweep net using the following equation (Anteau and Afton 2008):

$$VS = 2(\sum D_i) \times SN,$$

where D_i = depth at each sampling location and SN = area of the sweep-net opening (0.072 m^2). Vegetation or debris that was brought up in the sweep net was included in the sample, unless >50% of the object was hanging outside the net. I composited the samples into 10- and 60-m samples for each wetland, and samples were chilled with ice then frozen within 8 hours of collection. In the laboratory, I allowed the samples to thaw, and then I sorted and counted invertebrates by taxonomic level (Table 4.1). I estimated dry biomass of aquatic invertebrates (g m^{-3}) for each wetland using counts multiplied by an average mass for each taxon, a mass that was calculated from a long term wetland ecological study at Cottonwood Lake Study Area, North Dakota, using data collected in April–May during 1992–2012 (David Mushet, Northern Prairie Wildlife Research Center, U.S. Geological Survey, *personal communication*).

Wetland habitat

After a sweep-net sample had been taken at a station, I surveyed the abundance of submerged aquatic vegetation along a perpendicular sub-transect originating at the sampling station. I recorded vegetation presence/absence of 10 rake grabs (36-tine, 91.4 cm wide Lake Rake, Ben Meadows Co., Janesville, WI) spaced approximately 1 m apart on each sub-transect (Nyman and Chabreck 1996; Anteau and Afton 2008). One rake grab consisted of the rake being gently placed on the wetland bottom and then pulled straight up to the surface. The rake was cleaned of vegetation after each grab.

At four regularly spaced locations that approximated quarters of each wetland I measured turbidity (± 2 nephelometric turbidity units [NTU]), electrical conductivity (± 1µS), and water temperature (± 1ºC). These measurements were taken prior to any disturbance by other sampling methods.

Water depth

To estimate change in depth between surveys of 2004/05 (Anteau and Afton 2008) and 2011, I measured water depth (± 0.1 m) at 10 locations estimated to be 10 m into open water from 2004/05 the shoreline or emergent vegetation to open-water interface. When waves were present, I recorded the average depth between wave crests and troughs. Prior to field work, I delineated the shoreline or emergent vegetation to open-water interface of each wetland using imagery (National Agricultural Imagery Program, U.S. Department of Agriculture; hereafter NAIP) acquired in the summer (July) prior to each spring survey by Anteau and Afton (2008). I used the imagery from the previous year because it better represents the location of the emergent vegetation to open-water interface that Anteau and Afton (2008) used to locate their sampling locations. I digitized the interface by using GIS software at a scale of 1:5,000. I offset (i.e.

buffered) the digitized open-water interface by 10 m in the direction of the wetland center to approximate locations of 2004/05 sampling. I derived my 10 random points from the 10-m buffer, but I constrained point locations so there is a minimum distance of 40 m between points. I loaded the random points onto the Trimble GeoXT to navigate to sampling locations. Survey locations found within the emergent vegetation ring were recorded as such, because different dynamics of sedimentation and accumulation of organics were expected.

Table 4.1. Taxonomic names and rank to which aquatic invertebrates were sorted, counted, and biomass estimated. Taxonomic information retrieved 28 July 2014, from the Integrated Taxonomic Information System on-line database, http://www.itis.gov/.

Taxon	Taxonomic Rank	Taxon	Taxonomic Rank
Anisoptera	suborder	Gastropoda	class
Anostraca	order	Gyrinidae	family
Bivalvia	class	Haliplidae	family
Caenis	genus	Hirundinea	subclass
Callibaetis	genus	Hyalella	genus
Ceratopogonidae	family	Hydrophilidae	family
Chaoboridae	family	Laevicaudata	suborder
Chironomidae	family	Notonectidae	family
Cladocera	order	Ostracoda	class
Collembola	order	Pleidae	family
Copepoda	subclass	Prostigmata	suborder
Corixidae	family	Stratiomyidae	family
Culicidae	family	Tipulidae	family
Dytiscidae	family	Trichoptera	order
Gammarus	genus	Zygoptera	suborder

Spatial Data Preparation

Water surface area

I used water surface area delineated for each surveyed wetland by McCauley et al. (In Review) using photointerpretation of NAIP aerial imagery from 2010, to approximate the wetland water surface area during spring 2011. Photointerpretation was performed while images were viewed as panchromatic instead of true-color, because they were done as part of a larger study that involved panchromatic imagery (see McCauley et al. In Review). Where the waterline was obscured by emergent vegetation, the waterline was approximated to be halfway between the emergent-vegetation to open-water interface and clearly identifiable upland.

Catchments

I used wetland catchments as an index of watershed derived wetland complexes defined as the portion of the landscape in which surface water flows into a focal wetland, and included more-intermittent wetlands and their catchments (McCauley et al. In Review). Catchments were derived for each of the surveyed wetlands using high-resolution digital elevation model (DEM; source data: 3 m pixel lidar; Data available from the U.S. Geological Survey or 5 m pixel interferometric synthetic aperture radar from Intermap Technologies, Inc., Englewood, Colorado) and surface hydrology modeling tools by McCauley and Anteau (2014). Some catchments (46%) that were large or highly irregular in shape were truncated to a 2.5 km maximum radius from the wetland basin for logistical reasons associated with assembling landscape variables, such as amount of wetland area drained. The 2.5-km radius encompassed >90% of the total catchment area for 68% of catchments. Landscape conditions within these 2.5-km truncated catchments should represent the condition of the full catchment, and the conditions nearest the wetland basin likely influence the basin most. Therefore, I assumed the 2.5-km-

truncated catchment provided a reasonable area to evaluate impacts of land use in our system and are an improvement over the simply buffering around a wetland a set distance, a common practice (McCauley and Anteau 2014).

Catchment drainage

I used an index that estimated the percent catchment area that was drained wetland during 2003–2010 using multiple data sources, including: aerial photographs, DEM, NWI, and spatially explicit soil data (McCauley et al. In Review). Wetlands were identified as drained if they were present in historical photographs (dating back to 1937) but not present in current photographs, or if the wetlands were identified as part of a drainage network. Significant drainage occurred prior to 2003 in our study area; however, there was negligible evidence of additional drainage after 2003.

Basin area

I defined a wetland basin as the topographic depression that collects surface water that which is isolated from basins of other wetlands of an equal or more permanent hydroperiod. Thus the basin area is the maximum water surface area of a wetland without water spilling and flowing out of the basin. I used the high-resolution DEMs (3 m pixel lidar or 5 m pixel IfSAR) to find the spill point of the basin and then delineated the area at that spill point elevation within the basin. Because I predicted that wetlands in basins that were near full or that were full would more likely have or be connected to deep water refugia, I calculated the proportion of the basin that the focal wetland filled in summer 2010 to approximate the condition in spring 2011.

Statistical Analyses

I evaluated the potential effect of water level and water-level dynamics on occurrence of fish in wetlands by using mixed effects logistic regression analyses (Package *lme4* for R

Statistical Computing Environment; R Development Core Team 2010; Bates et al. 2011). I separately analyzed presence/absence of fish of any species and specifically for fathead minnows. Specific effects I evaluated were maximum water depth observed in 2011, drainage within the catchment, and basin percent full. There was only weak evidence of correlation among independent variables ($|r| < 0.28$). I included township-cluster as a random effect.

I evaluated the same effects of water level and water-level dynamics on abundance of fish found in 2011 using mixed effects regression analyses (Package *lme4* for R Statistical Computing Environment; R Development Core Team 2010; Bates et al. 2011). I used catch per unit effort (natural logarithm +1) as a relative abundance response index in separate analyses of fish of all species and of fathead minnows. In an *a priori* model I evaluated the same independent variables as in the occurrence model, including: maximum water depth observed in 2011, drainage within the catchment, and basin percent full. I included township cluster as a random effect.

I used multivariate multiple regression analysis to evaluate the effect fish might have on wetland quality (R Statistical Computing Environment; R Development Core Team 2010). I evaluated the effect of fathead minnows separate from that of other fish species by using an independent variable for each group. I also included maximum depth and water surface area as additional independent variables to control for variation in size among wetlands. Dependent variables used to index wetland quality related to habitat for waterbirds included: turbidity, abundance of submerged vegetation, densities of amphipods and cladocerans, and total aquatic invertebrate biomass.

I compared each *a priori* model to an intercept only model to evaluate model goodness-of-fit. In each analysis, I interpreted importance and size of independent effects within models

using 95% confidence intervals. I considered effects with confidence intervals that did not overlap zero important.

Results

In 2011, fathead minnows, small fish, large fish and fish of any species were present in 45%, 38%, 17%, and 57% of 138 wetlands surveyed, respectively. This was an increase of 18%, 16%, 5%, and 14%, respectively, over that observed in 81 wetlands during 2004/05 (Anteau and Afton 2008; Anteau et al. 2011). Relative abundance of fathead minnows and other small fish increased in wetlands from 2004/05 to 2011, but we found only weak evidence of an increase in abundance of large fish for the same time period (Figure 4.2). Maximum wetland depth in 2011 ranged 0.2 m to >3.0 m (mean = 2.0 m, SD = 0.7). Wetland drainage within catchments of focal wetlands ranged from 0–13% (mean = 2.2%, SD = 2.6). On average in 2011, wetland topographic basins were 64% full (SD = 27; range = 1% to >100%).

Models used to explain occurrence of fish and specifically fathead minnows in 138 wetlands during 2011 both fit better than a null model (χ^2 = 13.09, df = 3, P = 0.004; χ^2 = 15.80, df = 3, P = 0.001; respectively). Probability of fish occurrence was positively correlated with greater wetland depth and water levels nearer the wetland basin spill elevation (Table 4.2). Probability of fathead minnow occurrence was positively correlated with greater percent catchment area that was drained wetland and water levels nearer the wetland basin spill elevation (Table 4.3).

Mixed effects regression models used to explain abundance of fish and specifically fathead minnows in 138 wetlands during 2011 both fit better than an intercept only model (χ^2 = 18.39, df = 3, P < 0.001; χ^2 = 11.76, df = 3, P = 0.008; respectively). These models explained 52% and 20% of the variability in abundance of fish and specifically fathead minnows in my

observations among wetlands. Township within which wetlands were surveyed accounted for 24% and 6% percent of the variation in fish and specifically fathead minnow abundance, respectively. Fish abundance was positively correlated with greater wetland depth and water levels nearer the wetland basin spill elevation (Table 4.4). Abundance of fathead minnows was positively correlated with water levels nearer the wetland basin spill elevation (Table 4.5).

The multivariate multiple regression model used to evaluate the effect of fathead minnows and other fish on wetland quality was better fitted than was an intercept only model (Pillai = 0.640, $F_{20, 528} = 5.031$, $P < 0.001$). Abundance of fathead minnows was correlated with increased turbidity and reduced abundance of submerged vegetation and invertebrate biomass (Tables 4.6). There was insufficient evidence to support any correlation of other fish species to these same parameters of wetland quality. I did not find sufficient evidence for fish abundance directly impacting density of amphipods or cladocerans. Maximum depth of a wetland was an important factor to control for turbidity, cladoceran density, and invertebrate biomass; and, water surface area an important factor to control for turbidity, submerged vegetation, and invertebrate biomass.

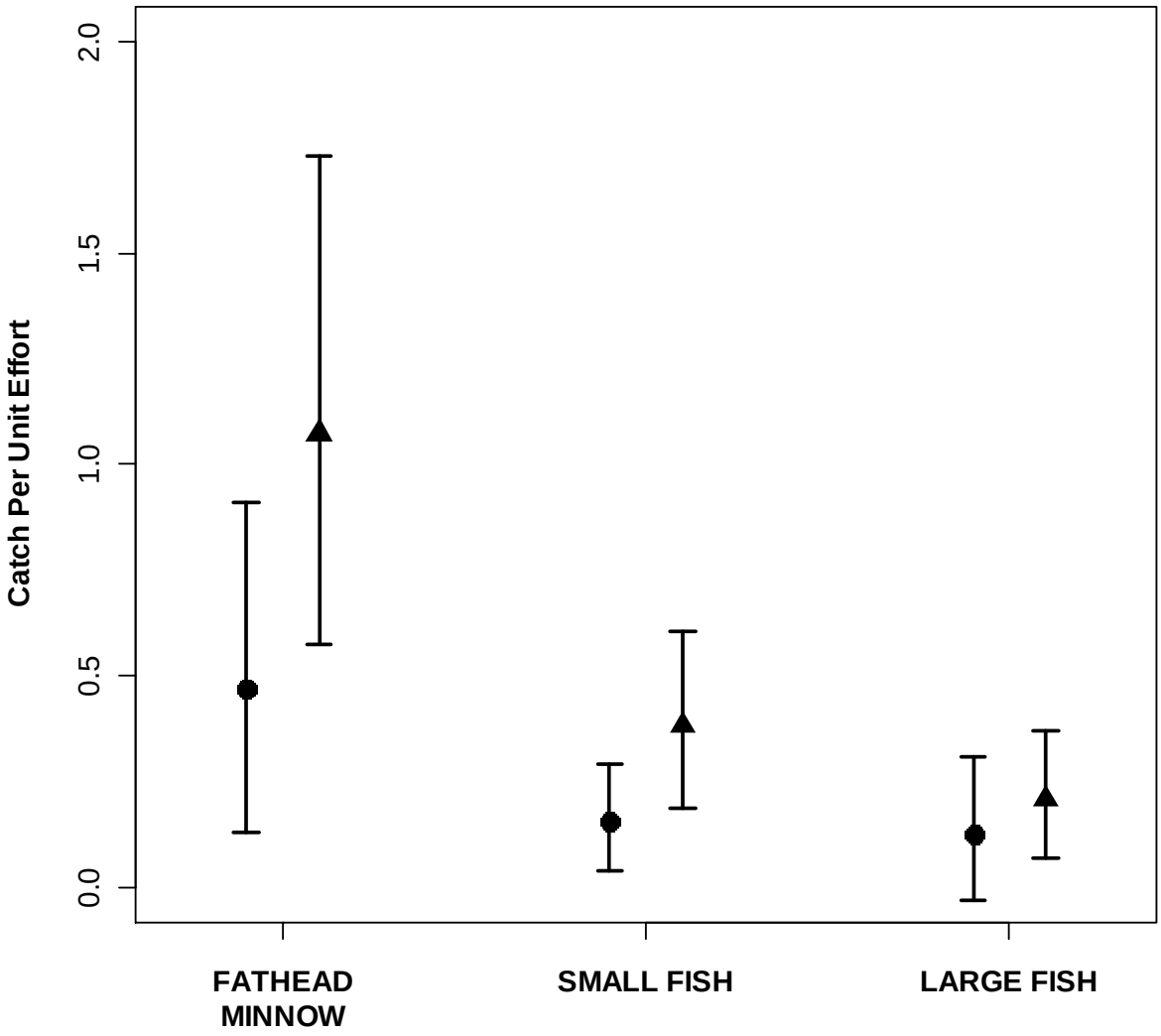

Figure 4.2. Back-transformed geometric least squares means of catch per unit effort (±95% CI) of fish groups during spring 2004 or 2005 (circles) and 2011 (triangles) within semipermanent and permanent prairie pothole wetlands (n = 81) in North Dakota. Fish groups are fathead minnows, small fish as other small species typically < 10 cm, and large fish as species typically > 10 cm in length.

Table 4.2. Fixed effect parameter estimates from an *a priori* mixed effects binomial model used to examine the effect of wetland hydrology and connectivity on probability of occurrence of fish within more-permanent wetlands during a climatic wet period during spring 2011 in North Dakota. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits.

Fixed Effect	$\hat{\beta}$	SE	LCL	UCL
Intercept	-1.351	0.835	-2.987	0.285
Max Depth	0.625	0.319	-0.001	1.252
Drainage	0.154	0.112	-0.066	0.374
Basin Full	0.020	0.009	0.003	0.036

Table 4.3. Fixed effect parameter estimates from an *a priori* mixed effects binomial model used to examine the effect of wetland hydrology and connectivity on probability of occurrence of fathead minnows within more-permanent wetlands during a climatic wet period during spring 2011 in North Dakota. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits.

Fixed Effect	$\hat{\beta}$	SE	LCL	UCL
Intercept	-1.905	0.741	-3.358	-0.451
Max Depth	0.031	0.259	-0.477	0.539
Drainage	0.217	0.085	0.051	0.383
Basin Full	0.018	0.007	0.004	0.032

Table 4.4. Fixed effect parameter estimates from an *a priori* mixed effects regression model used to examine the effect of wetland hydrology and connectivity on relative abundance of fish (catch per unit effort) within more-permanent wetlands during a climatic wet period during spring 2011 in North Dakota. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits. A colon indicates an interaction predictor term.

Fixed Effect	$\hat{\beta}$	SE	LCL	UCL
Intercept	-0.454	0.231	-0.908	-0.001
Max Depth	0.231	0.082	0.071	0.392
Drainage	0.031	0.025	-0.018	0.080
Basin Full	0.007	0.002	0.003	0.011

Table 4.5. Fixed effect parameter estimates from an *a priori* mixed effects regression model used to examine the effect of wetland hydrology and connectivity on relative abundance of fathead minnows (catch per unit effort) within more-permanent wetlands during a climatic wet period during spring 2011 in North Dakota. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits.

Fixed Effect	$\hat{\beta}$	SE	LCL	UCL
Intercept	-0.340	0.209	-0.749	0.069
Max Depth	0.122	0.075	-0.025	0.269
Drainage	0.017	0.022	-0.025	0.060
Basin Full	0.006	0.002	0.002	0.010

Table 4.6. Parameter estimates from an *a priori* multivariate multiple regression model used to examine the effect of fathead minnows and fish of other species on quality of 138 more-permanent wetlands in North Dakota during spring 2011. Wetland quality was defined as low turbidity, greater abundance of submerged vegetation, greater densities of amphipod or cladocerans, and greater aquatic invertebrate biomass. Maximum depth and water surface area were used to control for wetland size. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits.

Response	Predictor	$\hat{\beta}$	SE	LCL	UCL
Turbidity	Intercept	21.363	7.090	7.467	35.260
	Fathead Minnow	2.735	0.709	1.347	4.124
	Other Fish	0.079	1.925	-3.694	3.851
	Max Depth (m)	-9.797	3.331	-16.325	-3.269
	Surface Area (*ln* ha)	4.355	1.651	1.119	7.591
Submerged Vegetation	Intercept	8.542	0.881	6.816	10.268
	Fathead Minnow	-0.209	0.088	-0.381	-0.036
	Other Fish	0.083	0.239	-0.386	0.551
	Max Depth	-0.777	0.414	-1.587	0.034
	Surface Area	-0.952	0.205	-1.354	-0.550
Amphipods	Intercept	2.036	0.518	1.020	3.052
	Fathead Minnow	0.005	0.052	-0.096	0.107
	Other Fish	0.025	0.141	-0.251	0.301
	Max Depth	0.329	0.244	-0.148	0.806
	Surface Area	-0.098	0.121	-0.334	0.139
Cladocerans	Intercept	3.137	0.597	1.967	4.308
	Fathead Minnow	0.010	0.060	-0.107	0.127
	Other Fish	-0.242	0.162	-0.560	0.075
	Max Depth	-0.911	0.281	-1.461	-0.361
	Surface Area	0.217	0.139	-0.056	0.490
Invertebrate Biomass	Intercept	1.846	0.412	1.038	2.654
	Fathead Minnow	-0.097	0.041	-0.177	-0.016
	Other Fish	0.042	0.112	-0.178	0.261
	Max Depth	-0.461	0.194	-0.840	-0.081
	Surface Area	-0.417	0.096	-0.605	-0.229

Discussion

My results provide support for the hypothesis that consolidation drainage has caused an increase in dispersal of fish and creation of more deep-water refugia where fish are in higher abundance and can serve as source populations for further dispersal during period of wet climate conditions (Zimmer et al. 2001a; Anteau 2012). Thus, increased presence and abundance of fish can be associated to consolidation drainage by the evidence that suggests progressive increases in water level, less water-level fluctuation in response to climate variability, and ultimately more connectivity amongst wetlands to larger watersheds as a result of drainage within the catchments of wetlands (McCauley et al. In Review; Chapter 2). These results are consistent with those of others that have explained presence of fish as a function of wetland depth and connectedness, and climate variability (Tonn and Magnuson 1982; Rahel 1984; Magnuson et al. 1998; Hanson et al. 2005; Herwig et al. 2010). Moreover, the impact of consolidation drainage on wetland hydrology combined with evidence herein of sustained fish populations suggests that fish populations are likely to be more-permanent in more wetlands within modified landscapes.

The overall increase in wetland depth that I observed provided more deep-water habitat that was more suitable for fish to survive and allowed fish to colonize into more wetlands through connections created by higher water-levels. I observed fish in more wetlands and in higher abundances than had been observed in the past (Peterka 1989; Anteau and Afton 2008; Anteau et al. 2011). Further, these increases were correlated with wetlands that filled more of their topographic basin. While in the short term, some of the observed increases in fish could be due to prolonged wet climate conditions; over the long-term it appears that consolidation drainage has potential to permanently increased fish occurrence and abundance. If the climate were to shift towards more severe dry periods perhaps these trends may be reversed; however, it

is unclear what level of drought is required to reverse the trends in increasing water level due to consolidation drainage (McCauley et al. In Review; Chapter 2). Long-term fish community trends that include a more-severe dry period as part of a longer period climate cycle will help to evaluate the permanence of the effects from consolidation drainage.

Numerous studies have linked presence of fish in wetlands to increased turbidity, reduced submerged vegetation, and reduced abundance of invertebrates (e.g., Scheffer et al. 1993; Hanson and Butler 1994; Zimmer et al. 2001a; Anteau et al. 2011; Maurer et al. 2014). It is perhaps safe to assume that fish have a direct negative affect on invertebrate abundance when they forage upon them (e.g., Hanson and Riggs 1995). However, I did not observe a direct decrease in amphipod or cladoceran abundance linked to abundance of fish, perhaps because during an expansion of fish wetlands with good invertebrate abundance also result in great abundances of fish. My observations were consistent with an indirect mechanisms where greater fathead minnow abundance results in an increase in turbidity and a decrease in submerged vegetation which in turn results in a decrease in overall invertebrate biomass including amphipods, because there was evidence that amphipod abundance was positively related to submerged vegetation and negatively related to turbidity (Anteau et al. 2011; Chapter 5). Maurer et al. (2014) also found support for this indirect relationship within wetlands in Iowa. While evidence from studies that provide snapshots of many wetlands suggests fish have an indirect impact on aquatic invertebrate communities through increased turbidity and decreased abundance of submerged vegetation and overall invertebrate biomass, long-term studies of fewer wetlands or lakes have provided an opportunity to observe stages of changes in trophic structure as a result of fish introduction and eliminations (Carpenter et al. 1985; Hanson and Butler 1994). Nonetheless, increased permanence and greater abundance of fish, specifically fathead minnows,

in prairie pothole wetlands can be associated with negatively impacting the quality of a wetland to support waterbird populations that rely on macroinvertebrate prey.

My results also indicated that small wetlands and shallow wetlands had greater invertebrate biomass than large wetland and deep wetlands. Increased water level and hydroperiod resulting from consolidation drainage are likely to continue to effect wetland communities across the region, unless management actions are taken to restore complexes of wetlands having various hydroperiods and more surface isolation. Increased fish abundance and turbidity, which are linked to consolidation drainage, can serve as a negative indicator of wetland quality to support waterbirds. Accordingly, evaluation of distributions of fish and turbidity within wetlands across landscapes could provide a regional-scale assessment of wetland quality. If the availability of quality wetlands that can support waterbirds continues to decrease, the effects are likely to become more noticeable in waterbird populations that rely on invertebrates within these wetlands to obtain nutrients required for migration and breeding (Afton and Anderson 2001; Anteau and Afton 2004).

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CHAPTER 5. AMPHIPOD DENSITIES REMAIN LOW FOLLOWING WATER-LEVEL FLUCTUATION IN PRAIRIE POTHOLE WETLANDS

Abstract

Variability in amphipod abundance and productivity within wetlands of the Prairie Pothole Region is thought to have been historically driven by inter-annual fluctuations of water levels that facilitated nutrient cycling. However, landscape modifications have altered wetland hydrologic regimes and responses to climate variability, namely water-level fluctuation. Consequent changes in amphipod abundance and productivity may impact waterbird populations, because amphipods are important forage for migrating and breeding waterbirds in the region. In 2004–2005, amphipods densities were low across the Prairie Pothole Region following a period of high and stable water levels, perhaps due to lack of water-level fluctuation. I tested whether subsequent water-level fluctuations in the prairie pothole wetlands in North Dakota influenced a change in density of *Gammarus lacustris* and *Hyalella azteca* (hereafter *Gammarus* and *Hyalella*, respectively) from prior to a dry period in 2006–2008 to after wetlands re-flooded in 2010–2011. Wetland water surface area decreased 22% (±2.0S E) during the dry period, and then wetlands re-flooded to 7% (±1.1 SE) greater than initial area during the wet period. However, *Gammarus* and *Hyalella* densities remained generally low in North Dakota; specifically, *Gammarus* densities did not change and *Hyalella* decreased slightly. Further, density of both species decreased where extensive historical wetland drainage occurred within catchments of surveyed wetlands; however, both species increased where wetlands filled more of their topographic basins. My findings suggest that previously reported low region-wide densities of amphipods were not a result of a sustained wet period; rather they may be the result of landscape modifications that alter wetland hydrology.

Introduction

Amphipods are a common crustacean in semipermanent and permanent wetlands of the Prairie Pothole Region, and *Gammarus lacustris* and *Hyalella azteca* (hereafter *Gammarus* and *Hyalella*, respectively) are the two most abundant species within wetlands of the region (Kantrud et al. 1989; Anteau and Afton 2008). The density of amphipods can serve as an indicator of wetland and water quality because amphipods are sensitive to disturbances in uplands, invasive species, and contaminants (Grue et al. 1988; Tome et al. 1995; Duan et al. 2000; Anteau and Afton 2008; Hentges and Stewart 2010; Anteau et al. 2011). Rich in lipids and proteins, amphipods are an important forage for locally breeding waterbirds and for those bound for other breeding areas that must acquire and maintain nutrient reserves while migrating through the region (Batt et al. 1989; Swanson and Duebbert 1989; Anteau and Afton 2006, 2011). Amphipod densities in the spring are an indicator of forage availability for spring migrating and breeding waterbirds and indicate previous-year productivity and overwinter survival of amphipods (Lindeman and Clark 1999; Anteau and Afton 2009a). Therefore, the quality of a wetland to support waterbirds can be assessed in the spring using the density of adult amphipods that survived over winter (Anteau and Afton 2008).

Historically, water levels in wetlands fluctuated in response to climate fluctuations between wet and dry periods (Kantrud et al. 1989; Euliss et al. 1999; Euliss et al. 2004; Anteau 2012; McCauley et al. In Review). It is thought that hydrologic responses of wetlands to these wet–dry periods are one of the primary drivers of productivity and density of aquatic invertebrates in the prairie pothole wetlands (Euliss et al. 1999). High and stable water levels inhibit nutrient cycling, but the drying of wetlands or portions of wetlands allows for nutrient cycling and a subsequent pulse of productivity after wet conditions return (Euliss et al. 1999).

Similarly, wetlands likely receive increases in nutrients when uplands are inundated by extreme or consecutive wet years. Accordingly, temporal position within wet–dry periods likely affects abundance of aquatic invertebrates and ultimately populations of waterbirds that are dependent on the nutritional resources provided by prairie pothole wetlands. However, landscape modifications can alter water-level responses to climate variability (Post van der Burg et al. In Prep.; McCauley et al. In Review; Chapter 2), potentially disrupting linkages among wet–dry periods, wetland productivity, and waterbird populations (Batt et al. 1989).

Abundance and quality of wetlands in North Dakota has declined due to landscape modifications, primarily agriculture (Dahl 1990; Anteau and Afton 2008; Bartzen et al. 2010). A common agricultural practice aimed at increasing tillable acreage is to consolidate water from smaller, less-permanent wetlands into larger, more-permanent wetlands (Krapu et al. 2004; Anteau 2012). This practice alters hydrology of wetlands that receive consolidated water by increasing their size and changing the way wetlands respond to climate fluctuations (Anteau 2012; Post van der Burg et al. In Prep.; McCauley et al. In Review; Chapter 2). Wetlands with water levels that are near the topographic basin spill point have attenuated water-level fluctuation which can impact pulses of productivity once experienced in these wetlands.

Existing drainage networks and high water levels increase surface water connections among remaining wetlands that can serve as corridors for fish to distribute into new wetlands and find overwinter refugia. A high abundance of fish can both directly (through predation) and indirectly (e.g., through increased turbidity or reduction of submerged aquatic vegetation) impact density of invertebrates in wetlands (Hanson and Butler 1994; Zimmer et al. 2000; Hanson et al. 2005; Anteau and Afton 2008; Anteau et al. 2011). Tiger salamanders (*Ambystoma tigrinum*) in high abundance can also decrease densities of amphipods through predation (Olenick and Glee

1981; Kantrud et al. 1989; Macneil et al. 1999; Benoy 2005); although, native populations of tiger salamander also have been negatively impacted by upland modification (Balas et al. 2012; Mushet et al. 2014).

Conversion of uplands surrounding wetlands from grasslands to cropland may indirectly decrease quality of wetlands by increasing sediment delivered by runoff water and wind thereby increasing turbidity of the water (Gleason and Euliss 1998). Turbidity and high sediment loads reduce the abundance of submerged aquatic vegetation and invertebrates in wetlands (Gleason and Euliss 1998; Anteau and Afton 2008; Anteau et al. 2011). However, buffers of grassland between wetlands and tilled land can reduce the effect of sedimentation and negative impacts on invertebrate abundance (Castelle et al. 1994; Anteau et al. 2011).

In 2004–2005, amphipod densities were low across the Prairie Pothole Region compared to historical records (Anteau and Afton 2008), perhaps due to landscape modifications (Anteau and Afton 2008; Anteau et al. 2011). However, most of the region in the years prior to 2004 and 2005 experienced a regime of relatively high and stable water levels since 1993; therefore, amphipod numbers could have been low due to a period of little inter-annual water-level variation during which nutrients limited productivity (Euliss et al. 1999; Euliss et al. 2004). Many parts of the Prairie Pothole Region in North Dakota experienced moderate to severe drought during 2006–2008 (NCDC 2014), making it possible for basins to have lower water levels and subsequent nutrient cycling (Euliss et al. 1999). In spring 2009, wet conditions returned for most prairie wetlands in North Dakota. Thus, if amphipod densities were low in 2004–2005 due to the temporal position within wet–dry climate fluctuations, then I expected amphipod densities would increase after water levels increased in 2009. However, if landscape

modifications disturbed water-level fluctuations or have had other influences upon amphipods, I expected densities to remain low.

In this chapter, I tested if water-level dynamics effected the change in density of amphipods from prior to the dry period in 2006–2008 to after wetlands re-flooded. I also evaluated the influence of landscape modifications, the presence of fish and salamanders on the change in amphipod density.

Methods

Study Area

I returned to wetlands within the Prairie Pothole Region of North Dakota (Figure 5.1) that were previously randomly selected and surveyed once in 2004 or 2005 (hereafter, 2004/05) by Anteau and Afton (2008; n = 153). These were lacustrine semipermanent and shallow-water permanent wetlands (Cowardin et al. 1979) that must have had an open-water area larger than 120 m across to be surveyed in 2004/05. In 2004/05, if reselection in the field was necessary, the nearest suitable semipermanent wetland was surveyed. In each year 2010 and 2011, I returned to 126 of the original 153 wetlands. I did not survey the remaining wetlands because I could not gain permission to access private lands, or wetlands had been amalgamated with larger water bodies (e.g., Devils Lake). Based on National Wetland Inventory classification (NWI; U.S. Fish and Wildlife Service 2003), 67% of our wetlands were semipermanent, 3% seasonal, and the rest being permanent wetlands or shallow-water lakes. Those wetlands classified by NWI as seasonal were wetlands reselected in the field in 2004/05 that were more characteristic of semipermanent wetlands at time of field assessment.

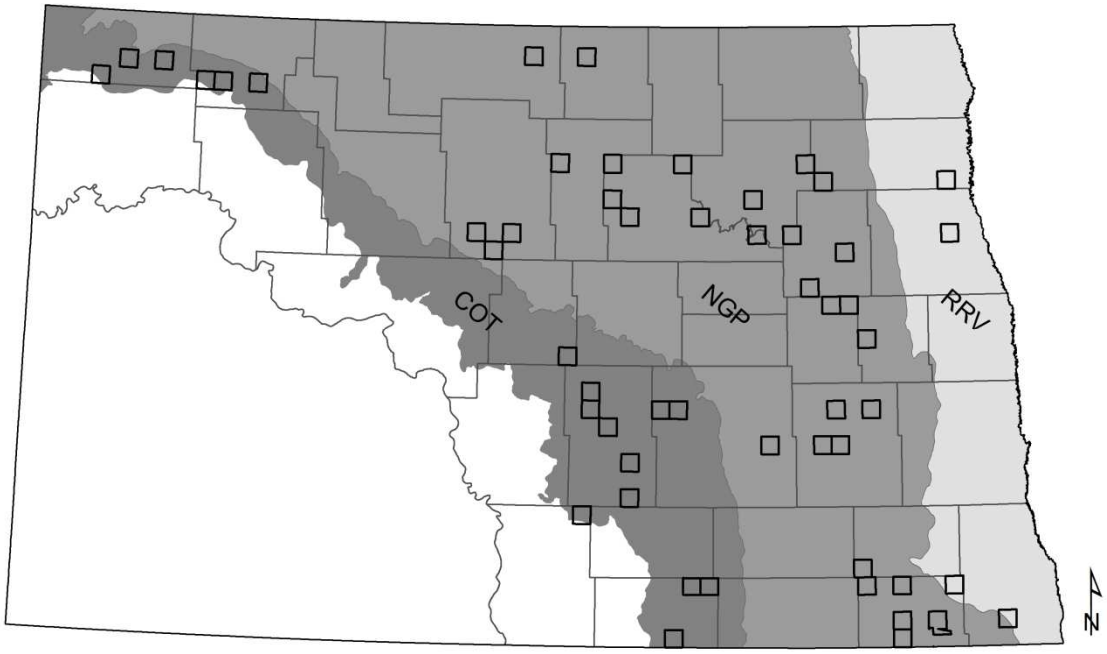

Figure 5.1. North Dakota study area showing townships where wetlands were surveyed during early spring of 2004, 2005, 2010 and 2011. Shaded areas are three physiographic regions of the Prairie Pothole Region: Red River Valley (RRV), Northern Glaciated Plains (NGP), and Missouri Coteau (COT).

Spring Wetland Surveys

During April and May of 2010 and 2011, I surveyed wetlands using techniques described in Anteau and Afton (2008) to collect data on amphipod density, fish abundance, water quality, and wetland vegetation structure. I collected data on randomly located transects extending from shoreline toward the center of the wetland. I recorded data electronically and georeferenced all sampling locations at the time of collection with a geographic information system (GIS) data logger (Trimble GeoXT, Trimble Navigation, Sunnyvale, CA).

Amphipod densities

I sampled amphipods in open water using a D-shaped sweep net (1,200 µm mesh, 0.072 m^2 opening, WARD'S Natural Science, Rochester, NY) at four amphipod-sampling transects (hereafter primary transects). Sampling stations at each transect were located at 10 and 60 m from the shoreline or emergent vegetation to open-water interface. Sample locations were adjusted along transects to ensure the station depth was between 0.5 and 3 m (see Anteau and Afton 2008). I recorded depth at each sampling station to the nearest 0.1 m. At each station, a sweet-net sample consisted of a sweep across the bottom for a distance equal to the water depth, and a sweep up through the water column. I calculated the volume of water sampled (VS; m^3) with a sweep net using the following equation (Anteau and Afton 2008):

$$VS = 2(\sum D_i) \times SN,$$

where D_i = depth at each sampling location and SN = area of the sweep-net opening (0.072 m^2). Vegetation or debris that was brought up in the sweep net was included in the sample, unless >50% of the object was hanging outside the net. I composited the samples into 10- and 60-m samples for each wetland, and samples were chilled with ice then frozen within 8 hours of collection. In the laboratory, I allowed the samples to thaw, and then I sorted and counted amphipods by species.

Wetland habitat

After a sweep-net sample had been taken at a station, I surveyed the abundance of submerged aquatic vegetation along a perpendicular sub-transect originating at the sampling station. I recorded vegetation presence/absence of 10 rake grabs (36-tine, 91.4 cm wide Lake Rake, Ben Meadows Co., Janesville, WI) spaced approximately 1 m apart on each sub-transect (Nyman and Chabreck 1996; Anteau and Afton 2008). One rake grab consisted of the rake being

gently placed on the wetland bottom and then pulled straight up to the surface. The rake was cleaned of vegetation after each grab.

At four regularly spaced locations that approximated quarters of each wetland I measured turbidity (± 2 nephelometric turbidity units [NTU]), electrical conductivity (± 1µS), and water temperature (± 1ºC). These measurements were taken prior to any disturbance by other sampling methods.

Fish and salamander communities

I used minnow traps and an experimental gill net in wetlands to determine relative abundance of fish and salamanders (see Anteau and Afton 2008). I set five Gee-style minnow traps with 6.35-mm mesh at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation is present) at five transects. I set the monofilament experimental gill net (21 × 2 m with seven 3-m panels ranging in mesh size from 1.9–7.6 cm) at a transect perpendicular to the shoreline with the small mesh end of the net at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation was present). Minnow traps and the gill net were deployed for 12–24 hours including an overnight period. At the time of trap and gill net retrieval, I sorted and counted fish by species and by length category (<5, 5–10, 10–20, 20–40, >40 cm) and measured body length of each salamander (±1 cm).

I classified all captures into one of four categories: fathead minnows (*Pimephales promelas*), other small fish species typically <10 cm (e.g., other minnows [Cyprinidae], darters [Anhingidae], and sticklebacks [Gasterosteidae]), large fish species typically >10 cm (e.g. northern pike [*Esox lucius*], walleye [*Sander vitreus*], yellow perch [*Perca flavescens*], sunfishes [*Lepomis* spp.], and bullhead and catfish [Ictaluridae]), and salamanders. I calculated catch per

unit effort (relative abundance) for each gear type by dividing the number of captures of each class by the hours the gear was in the water. For each class, I summed the quotients of the two gear types.

In 2011 I used the complete array of traps and a gill net in all wetlands surveyed. However, in 2010, I only used the five 6.35-mm mesh minnow traps in 75% of wetlands surveyed, and I did not adequately sample fish in the remaining 25% of wetlands. Therefore, I relied on the complete data collected in 2011 for my analyses.

Water depth

To estimate change in depth among surveys of 2004/05 (Anteau and Afton 2008) and surveys of 2010 and 2011, I measured water depth (± 0.1 m) at 10 locations estimated to be 10 m into open water from either the shoreline or emergent vegetation to open-water interface for 2004/05. When waves were present, I recorded the average depth between wave crests and troughs. Prior to field work, I delineated the shoreline or emergent vegetation to open-water interface of each wetland using imagery (National Agricultural Imagery Program, U.S. Department of Agriculture; hereafter NAIP) acquired in the summer (July) prior to each spring survey by Anteau and Afton (2008). I used the imagery from the previous year because it better represents the location of the emergent vegetation to open-water interface that Anteau and Afton (2008) used to locate their sampling locations. I digitized the interface by using GIS software at a scale of 1:5,000. I offset (i.e. buffered) the digitized open-water interface by 10 m in the direction of the wetland center to approximate locations of 2004/05 sampling. I derived my 10 random points from the 10-m buffer, but I constrained point locations so there is a minimum distance of 40 m between points. I loaded the random points onto the Trimble GeoXT to navigate to sampling locations. Sample locations found within the emergent vegetation ring

were recorded as such, because different dynamics of sedimentation and accumulation of organics were expected. Additionally, in 2011, I measured depth at four georeferenced locations where 10-m depth sampling occurred in 2010.

Water surface area

I used water surface area delineated for each surveyed wetland by photointerpretation of National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture) aerial imagery for 2003–2006 and 2009–2010 (McCauley et al. In Review). Photointerpretation was performed while images were viewed as panchromatic instead of true-color, because they were done as part of a larger study that involved panchromatic imagery (see McCauley et al. In Review). Where the waterline was obscured by emergent vegetation, the waterline was approximated to be halfway between the emergent-vegetation to open-water interface and clearly identifiable upland. NAIP imagery was not available for 2007 and 2008. For those years I used wetland water surface area delineated once in either 2007 or 2008 using high-resolution digital elevation model (DEM; source data: 1 m pixel lidar; Data available from the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR) orthorectified image (Intermap Technologies, Inc., Englewood, Colorado).

Catchments

I used wetland catchments as an index of watershed derived wetland complexes defined by McCauley et al. (In Review) that were delineated using high-resolution digital elevation models to detect the portion of the landscape where surface water flows into the focal wetland. These catchments included more-intermittent wetlands and their catchments (McCauley and Anteau 2014). DEM source data included 1 m pixel lidar (data available from the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR; Intermap

Technologies, Inc., Englewood, Colorado). I used catchment size in my analysis, but I also used the extent of the catchment to define the area to assess land use effects upon wetlands (McCauley and Anteau 2014). For logistical reasons associated with assembling landscape variables, such as amount of wetland area drained, I used catchments truncated to a 2.5 km maximum radius from the wetland basin for 46% of catchments because they were large or highly irregular in shape. The 2.5-km radius encompassed >90% of the total catchment area for 68% of catchments. Landscape conditions within these 2.5-km truncated catchments should represent the condition of the full catchment, and the conditions nearest the wetland basin likely influence the basin most. Therefore, I assume the 2.5-km-truncated catchment provided a reasonable area to evaluate impacts of land use in this system and are an improvement over the simply buffering around a wetland a set distance, a common practice (McCauley and Anteau 2014).

Catchment drainage

I used estimates of the percent of the catchment area that was drained wetland during 2003–2010 estimated from multiple data sources, including: aerial photographs, DEM, NWI, and spatially explicit soil data (see McCauley et al. In Review). Wetlands were identified as drained if they were present in historical photographs (dating back to 1937) but not present in current photographs, or if the wetlands were identified as part of a drainage network. Significant drainage occurred prior to 2003 in my study area; however, I found negligible evidence of additional drainage after 2003.

Basin area

Within a catchment, I defined the basin as the topographic depression that collects surface water and which is isolated from basins of other wetlands of an equal or more permanent hydroperiod. I calculated the maximum potential water surface area of each basin using the

high-resolution DEMs (3 m pixel lidar or 5 m pixel IfSAR) to find the elevation at which water flows out of the basin (i.e., spill point) and then delineated the area at that spill point elevation within the basin. Because I predicted that wetlands in basins that were near full or that were full would have less surface area dynamics, I calculated the proportion of the basin that the focal wetland filled at the start of each climate phase. I used a logit transformation of the proportion-basin-full variable × 0.1 for use in my analysis.

Statistical Analyses

I separately tested if *Gammarus* and *Hyalella* densities were different among years (i.e., position in climatic wet–dry fluctuations) and among regions using a two-way analysis of variance (ANOVA), including an interaction of the two factors. I included region in this *a priori* test because Anteau and Afton (2008) found differences in density by physiographic region, and it is possible that amphipod productivity varied by region during the period of study. Because amphipod densities followed a skewed-right distribution, I natural logarithm (+1)-transformed densities to meet assumptions of normality (Devore 2000). I calculated geometric least-squares mean density of both species for each year by region using estimates from the two-way ANOVA interaction. I plotted back-transformed geometric least-squares means and 95% confidence intervals. I evaluated main effects from back-transformed estimated means and 95% confidence intervals of two-way ANOVAs for each species that did not include the interaction. Means were interpreted as different if the confidence interval did not overall the mean of the other level.

For each *Gammarus* and *Hyalella*, I calculated the change in density for year one as the difference between the 2004/05 and 2010 samples, and for year two as the difference between the 2004/05 and 2011 samples. If a species was not found in any of the three sampling attempts, the wetland was removed from change in density analyses for that species. For both species, the

distribution of change in density had long tails, so I natural logarithm (+1) -transformed the absolute values of the difference and then resigned the transformed value. I analyzed data from two years of follow-up sampling (i.e., 2010 and 2011) to account for any lag in the productivity-response to fluctuating water levels; however, I expected amphipod colonization and production to be high during 2009 which was the first year of the wet period.

Prior to creating a general model for change in amphipod density, I evaluated changes in response to landscape modification and water-level fluctuation in year one and year two. Specifically, I calculated geometric least-squares mean changes in density separately for both species of amphipods in wetlands classified into categories delimited by one-third quantiles for 1) percent catchment area that was drained wetland; 2) percent wetland area that was re-flooded after drawdown during the drying period; and 3) percent wetland area that was newly flooded beyond 2003–2005 water levels. I interpreted an effect as present if the 95% confidence interval did not overlap zero. I plotted back-transformed geometric least-squares means and 95% confidence intervals.

To uncouple potential effects of landscape modifications from those of water-level fluctuations, I tested the effect of water-level fluctuation on changes in amphipod density for each species within a general mixed-effects regression analysis (Package *lme4* in R Statistical Computing Environment; R Development Core Team 2010; Bates et al. 2011). I evaluated water-level fluctuation effects in an *a priori* model by using natural logarithm (+1)-transformed area of wetland that was re-flooded after drawdown during the drying period and natural logarithm (+1)-transformed area of wetland that was newly flooded beyond 2003–2005 water levels. I included additional fixed effect variables to control for maximum depth observed in 2004/05, wetland connectedness by means of percent basin full and percent catchment area that

was drained wetland. I found only weak evidence of collinearity among fixed effects (all $|r| < 0.32$). I included a repeated measures term for wetland by year and a random effect term for sampled township in the models to accommodate my sampling design.

I conducted a second analysis on change in amphipod density that included only wetlands for which a complete set of fish abundance, salamander abundance, water-quality parameters and wetland vegetation variables were available in 2004/05 and 2011 samples. I created five variable suites representing alternative hypotheses as to influences on change in amphipod density, including: 1) water-level dynamics with re-flood area, newly flooded area, and basin full; 2) water quality with electrical conductivity, turbidity, and submerged aquatic vegetation abundance; 3) fish change in occurrence and/or change in density for any species; 4) fathead minnow change in occurrence and/or change in density; and, 5) salamander change in occurrence and/or change in density. Prior to creating multiple models I evaluated change in occurrence and change in density of fish, fathead minnows, and salamanders each separately in a full model that included all of the other suites. Change in occurrence resulted in the better model for each fish, fathead minnows, and salamander; therefore change in occurrence was used in all subsequent models. I created multiple models from all combination of variable suites, with the exception of change in occurrence of fish of any species and change in occurrence of fathead minnows being in the same model, and I included an intercept only model. I found only weak evidence of collinearity among fixed effect variables that were included in the same model (all $|r| < 0.40$). I used an information theoretical approach to select and interpret the single most parsimonious model using Akaike's Information Criterion adjusted for small sample size (AIC_C; Burnham and Anderson 2002).

I determined fixed effect variables to be important if 95% confidence intervals did not include zero. I reported goodness-of-fit for mixed effects models using marginal and conditional R^2 (Nakagawa and Schielzeth 2013).

Results

During 2010 and 2011, I resurveyed 126 wetlands that were initially surveyed in 2004/05 (Anteau and Afton 2008). At the time of initial sampling in 2004/05, wetlands averaged 63 ha of water surface area (range = 1–849 ha, median = 24 ha) and 1.3 m maximum water depth (range = 0.5–3.0 m, median = 1.0 m). During the dry period in 2006–2008, wetland water surface area had decreased 22% (±2.0 SE). During the following wet period in 2009–2011, average wetland water surface area was 16% (±1.7 SE) greater than the previously exposed area that had been re-flooded and 7% (±1.1 SE) greater than the initial area. On average, focal wetland basins were 61% (range = 1% to >100%, quartiles = 43%, 61%, 83%) and 65% (range = 1% to >100%, quartiles = 48%, 68%, 87%) full during 2010 and 2011, respectively. During 2011, focal wetland basins were 3% more full than during 2004/05 (range = -43% to 46%, quartiles = -4%, 2%, and 8%).

Gammarus were present in 34%, 25%, and 31% of wetlands in 2004/05, 2010, and 2011, respectively. The region-by-year interaction was not important for explaining *Gammarus* densities ($F_{4, 369} = 0.19$, $P = 0.94$; Figure 5.2). *Gammarus* densities were different among regions ($F_{2, 373} = 6.06$, $P < 0.01$), as densities were greater in NGP than in COT and RRV (Table 5.1). However, *Gammarus* densities did not differ among years ($F_{2, 373} = 0.85$, $P = 0.43$; Table 5.2).

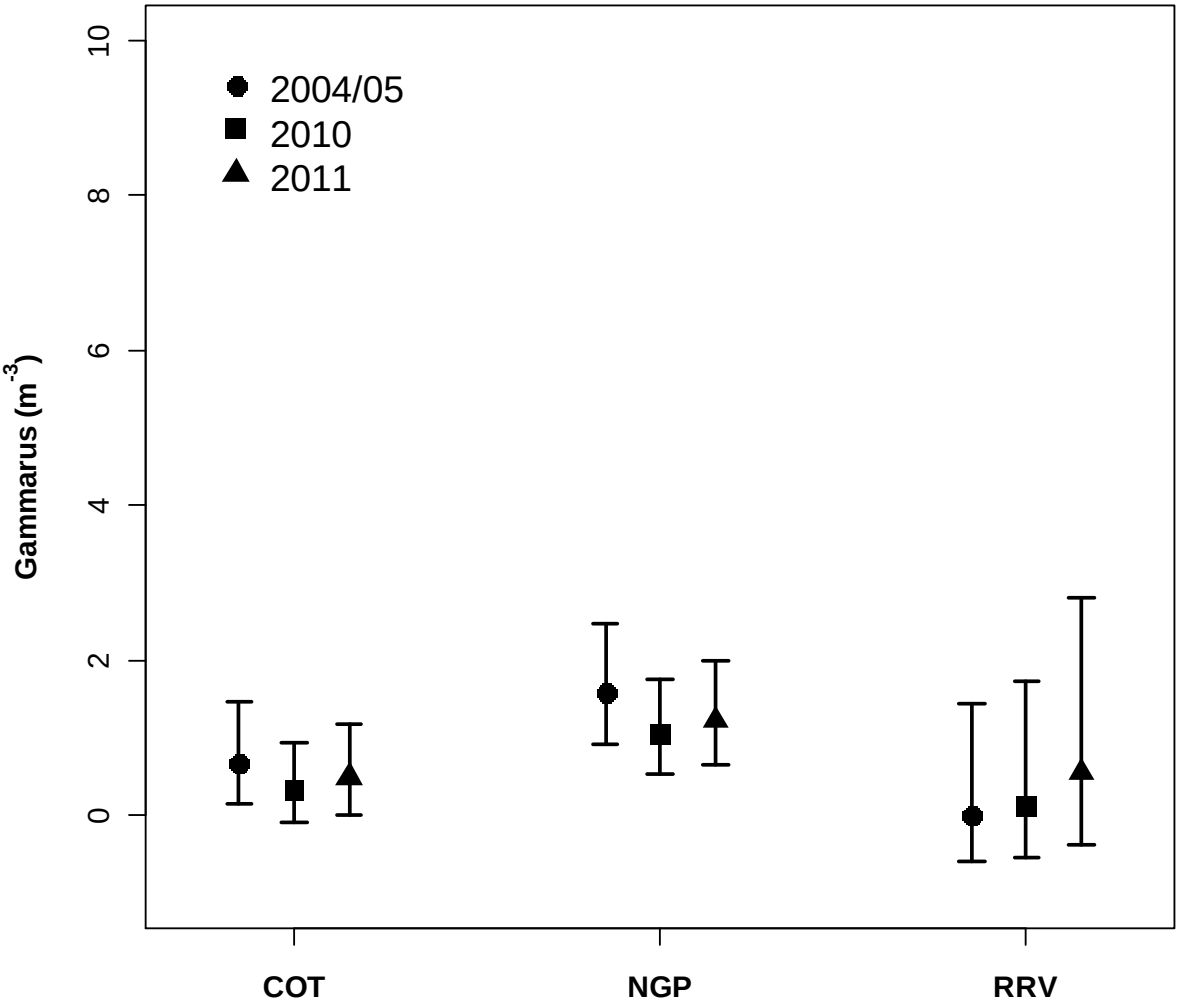

Figure 5.2. Back-transformed geometric least squares mean densities (m^{-3}) and 95% lower (LCL) and upper (UCL) confidence limits of *Gammarus lacustris* observed in 2004 or 2005 (circle), 2010 (square), and 2011 (triangle) in three physiographic regions of the Prairie Pothole Region of North Dakota: Red River Valley (RRV), Northern Glaciated Plains (NGP), and Missouri Coteau (COT).

Table 5.1. Back-transformed geometric least squares mean densities (m^{-3}) and 95% lower (LCL) and upper (UCL) confidence limits of *Gammarus lacustris* and *Hyalella azteca* observed during 2004 or 2005, 2010, and 2011 in N number of wetlands within three physiographic regions of the Prairie Pothole Region of North Dakota.

Region	N	Mean	LCL	UCL
Gammarus lacustris				
Missouri Coteau	44	0.49	0.20	0.86
Northern Glaciated Plains	74	1.28	0.93	1.70
Red River Valley	8	0.20	-0.28	1.01
Hyalella azteca				
Missouri Coteau	44	6.90	4.64	10.06
Northern Glaciated Plains	74	7.32	5.42	9.79
Red River Valley	8	5.40	1.91	13.09

Table 5.2. Back-transformed geometric least squares mean densities (m^{-3}) and 95% lower (LCL) and upper (UCL) confidence limits of *Gammarus lacustris* and *Hyalella azteca* observed in 126 wetlands within the Prairie Pothole Region of North Dakota.

Sampling Year	Mean	LCL	UCL
Gammarus lacustris			
2004 or 2005	1.10	0.67	1.63
2010	0.70	0.36	1.13
2011	0.89	0.51	1.37
Hyalella azteca			
2004 or 2005	9.76	6.62	14.18
2010	4.91	3.19	7.34
2011	7.17	4.79	10.53

Hyalella were present in 70%, 66%, and 79% of wetlands in 2004/05, 2010, and 2011, respectively. The region-by-year interaction was not important for explaining *Hyalella* densities ($F_{4, 369} = 0.52$, $P = 0.72$; Figure 5.3). However, *Hyalella* densities did differ among years ($F_{2, 373} = 2.94$, $P = 0.05$), as densities were greater in 2004/05 than in 2010 and densities in 2011 were marginally greater than 2010 (Table 5.2). Although, *Hyalella* densities did not differ among regions ($F_{2, 373} = 0.20$, $P = 0.82$; Table 5.1).

Overall changes in density of *Gammarus* and *Hyalella* in 2010 and 2011 compared to 2004/05 were relatively small; *Gammarus* (mean = -0.60 m^{-3}, 95% CI = -1.98 to 0.17 m^{-3}; mean = -0.28 m^{-3}, 95% CI = -1.40 to 0.45 m^{-3}; in 2010 and 2011, respectively) and *Hyalella* (mean = -1.52 m^{-3}, 95% CI = -3.83 to -0.32 m^{-3}; mean = -0.97 m^{-3}, 95% CI = -2.78 to -0.03 m^{-3}; in 2010 and 2011, respectively). However, there were large changes within some individual wetlands (Figure 5.4). Examination of landscape modification and water-level fluctuation effects revealed decreases in density of both *Gammarus* and *Hyalella* occurred in wetlands where a higher percent of the catchment area was drained wetland, initially where a small percent of the wetland was re-flooded after drawdown during the dry period, and for *Hyalella* only, where moderate expansion of the wetland occurred in 2010 (Figure 5.5).

Gammarus and *Hyalella* occurred in 50% and 92% wetlands, respectively, at least once during sampling in 2004/05, 2010, or 2011. Percent basin full was positively correlated with an increase in *Gammarus* density, and there was not sufficient evidence support percent wetland area re-flooded and newly flooded, maximum depth, and wetland drainage within the catchment as important to explain change in *Gammarus* density (Table 5.3). The mixed effects model used to explain change in density for *Gammarus* had a marginal R^2 of 10% and a conditional R^2 of 79%. Increase in *Hyalella* density was positively correlated with percent basin full and

negatively correlated with maximum depth, and there was not sufficient evidence support percent wetland area re-flooded and newly flooded, and wetland drainage within the catchment as important to explain change in *Hyalella* density (Table 5.4). The mixed effects model used to explain change in density for *Hyalella* had a marginal R^2 of 8% and a conditional R^2 of 75%.

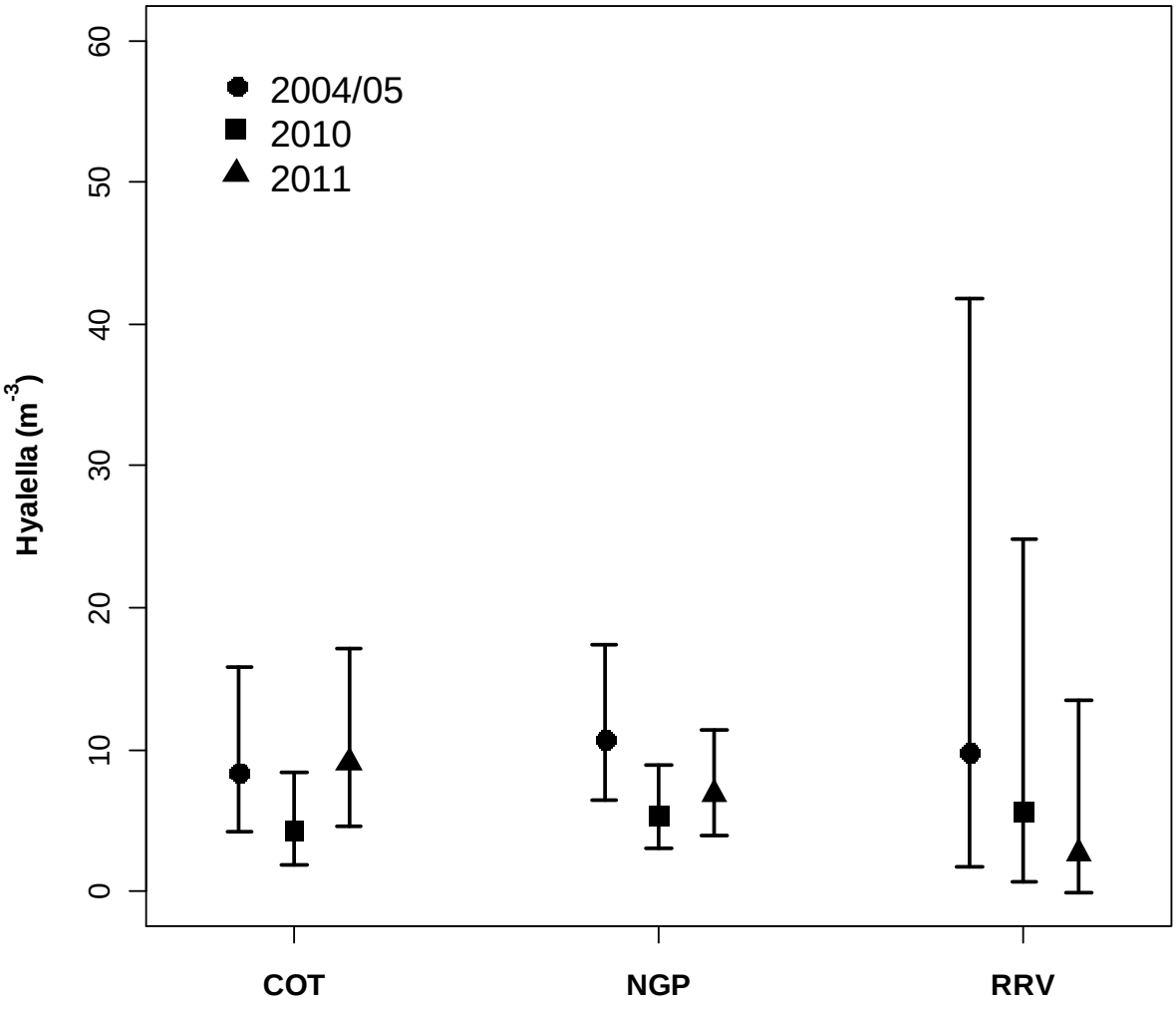

Figure 5.3. Back-transformed geometric least squares mean densities (m^{-3}) and 95% lower (LCL) and upper (UCL) confidence limits of *Hyalella azteca* observed in 2004 or 2005 (circle), 2010 (square), and 2011 (triangle) in three physiographic regions of the Prairie Pothole Region of North Dakota: Red River Valley (RRV), Northern Glaciated Plains (NGP), and Missouri Coteau (COT).

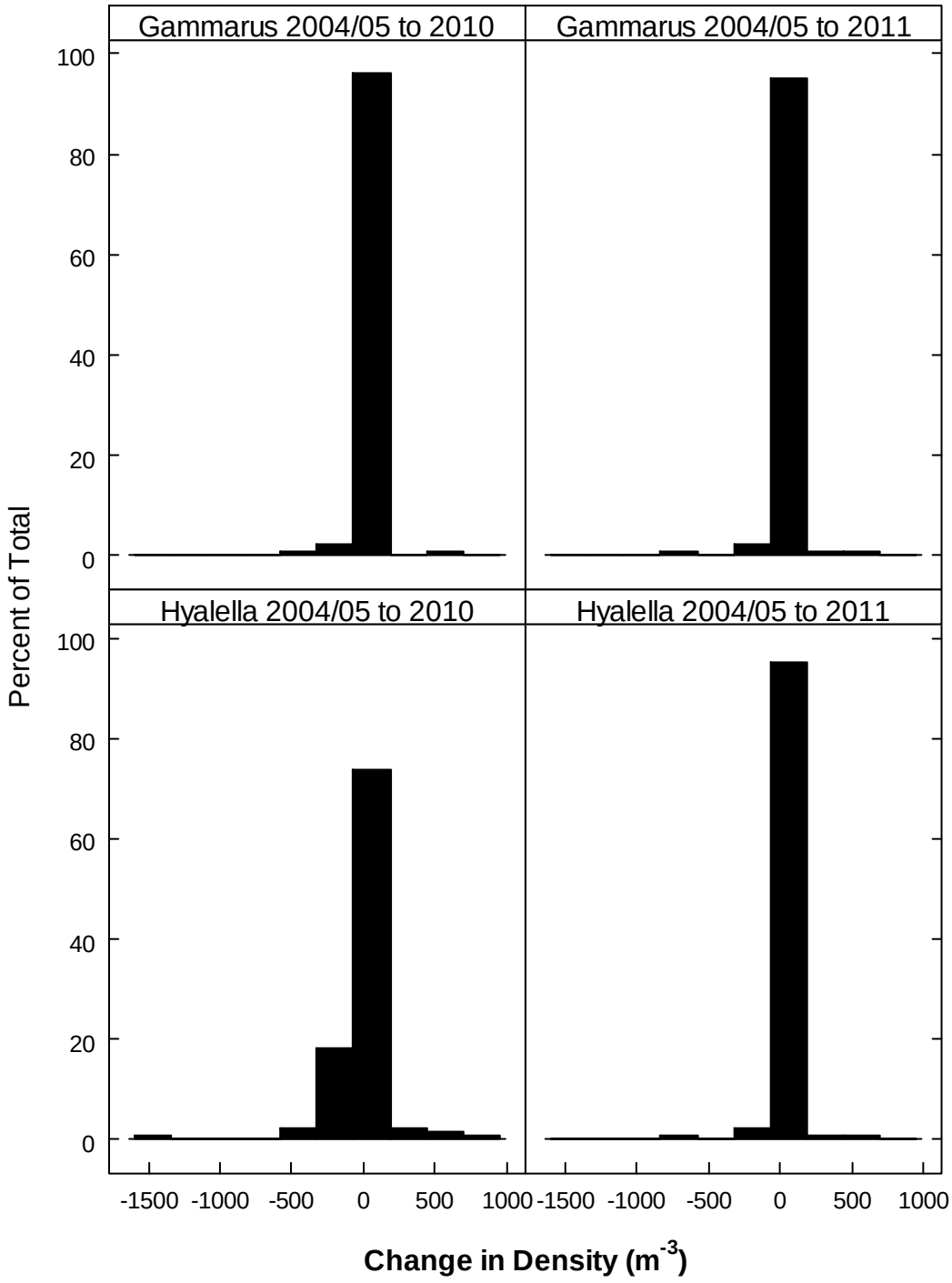

Figure 5.4. Distribution of change in density (m^{-3}) of *Gammarus lacustris* and *Hyalella azteca* from 2004 or 2005 to 2010 and 2011 observed in wetlands of the Prairie Pothole Region of North Dakota.

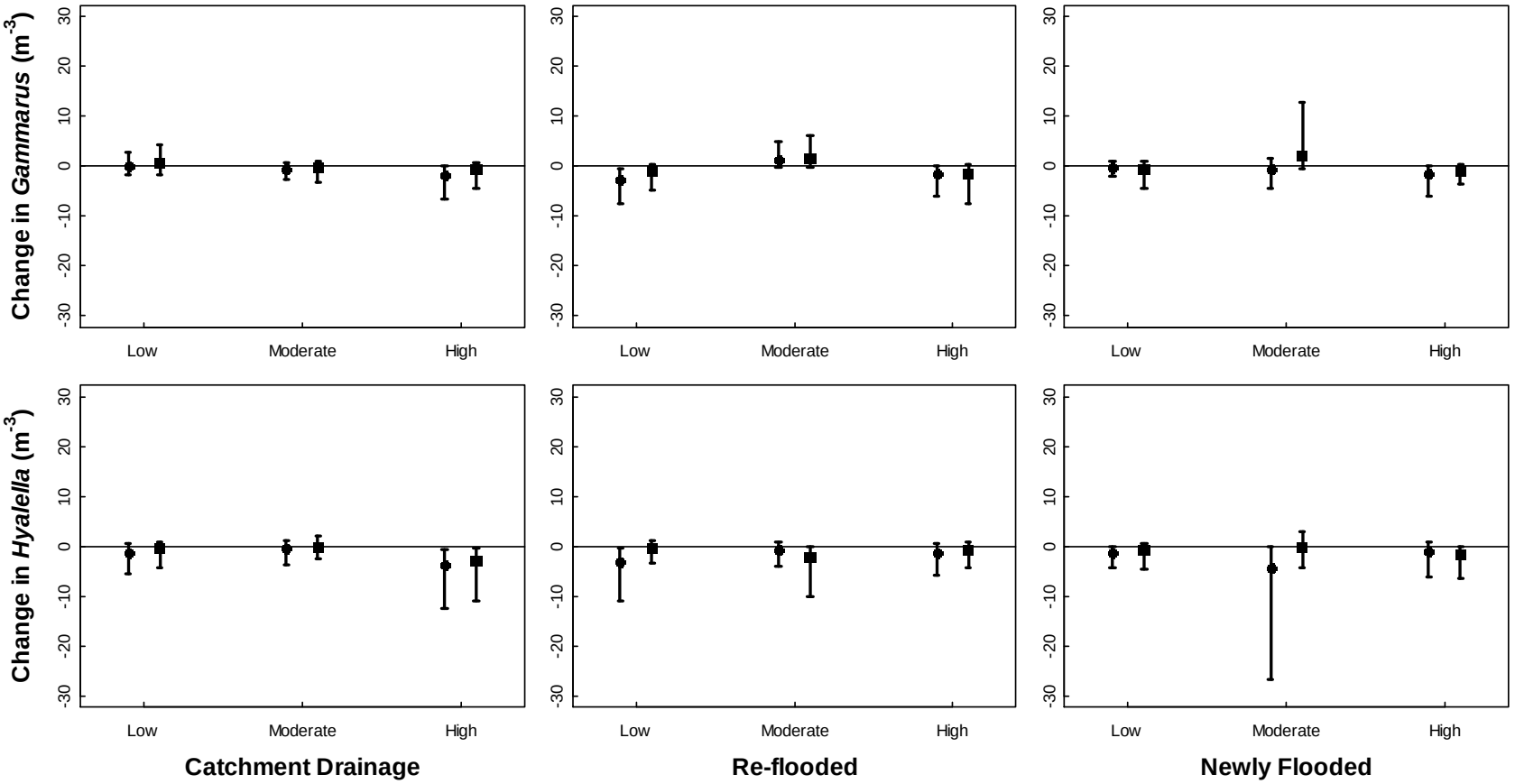

Figure 5.5. Back-transformed geometric least squares mean changes in density (m^{-3}) of *Gammarus lacustris* and *Hyalella azteca* from 2004 or 2005 to 2010 (circles) and 2011 (squares) observed in wetlands of the Prairie Pothole Region of North Dakota. Mean changes were estimated for levels delimited by one-third quantiles for percent catchment area that was drained wetland, percent wetland area after drawdown during the drying period, and percent wetland area that was newly flooded beyond 2003–2005 water levels.

Table 5.3. Estimated coefficients ($\hat{\beta}$) and standard errors for fixed effects within an *a priori* model used to examine the effect of water-level dynamics on change in density of *Gammarus lacustris* in wetlands of North Dakota from 2004 or 2005 to 2010 and 2011.

Fixed Effects	$\hat{\beta}$	SE	LCL	UCL
Intercept	-1.226	0.957	-3.101	0.650
Re-flooded	-0.109	0.258	-0.615	0.397
Newly Flooded	-0.215	0.181	-0.569	0.138
Maximum Depth	0.009	0.371	-0.719	0.736
Drainage	-0.154	0.134	-0.417	0.109
Basin Full	0.022	0.010	0.002	0.042

Table 5.4. Estimated coefficients ($\hat{\beta}$) and standard errors for fixed effects within an *a priori* model used to examine the effect of water-level dynamics on change in density of *Hyalella azteca* in wetlands of North Dakota from 2004 or 2005 to 2010 and 2011.

Fixed Effects	$\hat{\beta}$	SE	LCL	UCL
Intercept	-0.564	0.895	-2.318	1.191
Re-flooded	-0.201	0.260	-0.710	0.309
Newly Flooded	0.032	0.230	-0.418	0.483
Maximum Depth	-1.058	0.401	-1.844	-0.273
Drainage	-0.163	0.106	-0.371	0.046
Basin Full	0.025	0.011	0.005	0.046

Gammarus and *Hyalella* occurred in 49 and 76 of 81 wetlands, respectively, for which a complete set of fish abundance, salamander abundance, water-quality parameters and wetland vegetation variables were available in the 2004/05 and 2011 samples. The best model to explain changes in *Gammarus* included change in fish occurrence and change in salamander occurrence, and this model had more support than an intercept only model (Table 5.5). Increase in *Gammarus* density was positively correlated with occurrence of salamanders ($\hat{\beta}$ = 1.706, SE = 0.662, 95% CI = 0.408–3.004) and negatively correlated with occurrence of fish of any species ($\hat{\beta}$ = -3.164, SE = 0.773, 95% CI = -4.679 to -1.648). None of the models assembled from *a priori* variable suites had more support than an intercept only model to explain changes in *Hyalella* density (Table 5.6).

Table 5.5. Model selection results from alternative models composed of combinations of *a priori* variable suites, including water-level dynamics, water quality, change in occurrence of fish, salamander, or fathead minnows, used to examine their effect on change in density of *Gammarus lacustris* in wetlands of North Dakota from 2004 or 2005 to 2011. Reported are: model log likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small sample size (AIC_C), increase over lowest AIC_C (ΔAIC_C), and Akaike model weight (w_i) for models ($w_i \geq 0.01$) and an intercept only model.

Variable Suites	LL	K	AIC_C	ΔAIC_C	w_i
Fish, Salamanders	-104.97	8	229.54	0.00	0.77
Water-level Dynamics, Fish, Salamanders	-101.58	11	232.30	2.76	0.19
Water Quality, Fish, Salamanders	-103.88	11	236.89	7.35	0.02
Intercept Only	-112.86	6	239.73	10.19	0.00

Table 5.6. Model selection results from alternative models composed of combinations of *a priori* variable suites, including water-level dynamics, water quality, change in occurrence of fish, salamander, or fathead minnows, used to examine their effect on change in density of *Hyalella azteca* in wetlands of North Dakota from 2004 or 2005 to 2011. Reported are: model log likelihood (LL), number of estimated parameters (K), Akaike's Information Criterion for small sample size (AIC_C), increase over lowest AIC_C (ΔAIC_C), and Akaike model weight (w_i) for models ($w_i \geq 0.01$) and an intercept only model.

Variable Suites	LL	K	AIC_C	ΔAIC_C	w_i
Intercept Only	-201.70	6	416.62	0.00	0.33
Fathead Minnows	-200.75	7	417.14	0.52	0.26
Fish, Salamanders	-199.67	8	417.49	0.87	0.22
Salamanders	-201.49	7	418.62	2.00	0.12
Water-level Dynamics	-200.68	9	422.09	5.47	0.02
Water-level Dynamics, Fathead Minnows	-199.78	10	422.95	6.33	0.01
Water-level Dynamics, Fish, Salamanders	-198.71	11	423.54	6.92	0.01
Water Quality	-201.61	9	423.96	7.34	0.01
Water-level Dynamics, Salamanders	-200.40	10	424.18	7.56	0.01
Water Quality, Fathead Minnows	-200.64	10	424.66	8.04	0.01

Discussion

While overall amphipod densities during spring 2010 and 2011 generally were similar to those low values during spring 2004 and 2005 (Anteau and Afton 2008), there were changes within individual wetlands that provided some insight into factors that influenced change in amphipod density. I found weak evidence that high levels of historical wetland drainage within catchments of remaining wetlands negatively impacted densities of both *Hyalella* and *Gammarus*. I also found evidence of greater increases in both species of amphipod within

wetlands that filled more of their topographic basins; this might be related to more-full basins having or being connected to deeper-water overwintering habitat. However, my data also suggests that *Hyalella* were less abundant in wetlands of greater depth. This could be associated to differences in other *Hyalella* habitat characteristic that are coincident with greater wetland depth, such as structure of submerged aquatic vegetation communities, or those wetlands becoming suitable for fish. However, fish did not appear to be important in explaining changes in *Hyalella* densities.

Water levels in wetlands fluctuated in response to wet–dry periods, but the influence of climate variability on water-level fluctuations differed depending upon the amount of wetland drainage within the catchment (Chapter 2). Wetlands within catchments with more historical wetland drainage experienced less drawdown and more flooding than those in less drained catchments (<2% area drained). However, I did not find evidence of increased amphipod densities in wetlands where water-level fluctuations occurred whether it be new flooding terrestrial areas or re-flooding of dried wetland shore. Perhaps there is a more direct negative influence limiting amphipod densities than are nutrients limiting amphipod densities in these wetlands.

Amphipods are highly productive and capable of producing multiple broods within a breeding season (Covich and Thorp 1991; Wen 1992; Pickard and Benke 1996); therefore, it is unlikely that sampling in 2010 and 2011 was too early after the drawdown to observe a pulse in productivity of *Gammarus* and *Hyalella* in response to cycling of nutrients. Having an R-selected life history (Pianka 1970), it is likely that amphipod densities would respond to improved hydrologic and nutrient conditions within the first two years following of the wet period. Accordingly, I believe my study duration captured the important changes in amphipod

densities that can be attributed to the rewetting event of 2009. While mean amphipod densities were lower in 2010 than in 2011 in some instances, the difference is more likely a result of a further increase in water levels that increased the number of wetlands suitable habitat for overwinter survival of amphipods. Indeed, I observed overwinter survival of amphipod populations of both species in more wetlands in 2011 than in 2010. An increase in wetlands suitable for overwinter survival can contribute to improved amphipod densities across landscapes within the region. Perhaps of more importance to waterbird conservation is understanding what factors limit amphipod productivity within individual wetlands and how some wetlands can support extremely high densities of amphipods.

Historical estimates of amphipod densities are too sparse to allow for rigorous quantitative comparisons with current densities. However, Anteau and Afton (2008) concluded that densities in 2004 and 2005 likely had declined from historical levels based on comparisons with available amphipod data and marked shifts in lesser scaup diets away from amphipods to lesser-preferred foods (Anteau and Afton 2006; Strand et al. 2008; Anteau and Afton 2009a) and concurrent declines in lipid reserves and lipid acquisition of lesser scaup during spring migration (Anteau and Afton 2004, 2009b, 2011). I quantitatively evaluated our estimates in relation to those of Anteau and Afton (2008) in North Dakota, and our estimates are similar to those reported low estimates. Accordingly, my results suggest that the potential decline in amphipod densities in North Dakota that Anteau and Afton (2008) observed was not driven by the temporal position between wet–dry periods when data were collected.

During 2010–2011 there were more ideal hydrologic conditions than that during 2004–2005. I expected wetlands with high water-levels following the dry period in 2006–2008 to contain greater nutrient concentrations that would benefit wetland productivity. Indeed, I did

observe water-level fluctuations during the climatic wet–dry periods in wetlands with less drainage within their catchment, yet finding little overall change in amphipod density between sampling periods perhaps suggests either 1) that amphipod densities are now less tied to temporal position in climate wet–dry fluctuations than they were previously or 2) amphipods are not as responsive to climate as predicted. Although extremes of climate conditions that occur across decades likely do effect amphipod populations by temporarily reducing available suitable habitat, long-term declines in amphipod density across the region are more likely a result of landscape modifications that affect wetland hydrology, increased sedimentation, eutrophication, and increased agrochemical residues entering wetlands (Grue et al. 1988; Gleason and Euliss 1998; Anteau et al. 2011). Thus availability of suitable habitat for amphipods in lacustrine wetlands may be more-permanently reduced.

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CHAPTER 6. A LANDSCAPE-SCALE EVALUATION OF THE "ALTERNATIVE STABLE STATE" HYPOTHESIS WITHIN LARGE NORTHERN PRAIRIE WETLANDS IN CONTEXT OF WATERBIRD CONSERVATION

Abstract

Trophic structure of wetlands can be a useful indicator of their biological productivity, biodiversity, and overall perceived quality. The "alternative stable states" hypothesis suggests ecosystems can exist in discrete alternative trophic structures. In wetlands, alternative states include a clear state where primary productivity is dominated by macrophytes and a turbid state where primary productivity is dominated by phytoplankton. Chlorophyll *a* (chl *a*) concentration in water is commonly used to indicate trophic structure in wetlands because it is a key pigment in phytoplankton. I conducted a landscape-scale evaluation of the alternative stable state hypothesis by examining the distribution of remotely-sensed chl *a* concentrations during 2011 within 978 randomly selected semipermanent and permanent wetlands in the Prairie Pothole Region of North Dakota. Under the alternative stable states hypothesis I predicted that two alternative states should be observable as a bimodal distribution in a large sample of wetlands. Additionally, I evaluated how wetland chl *a* concentrations were related to consolidation drainage, upland land use, and fish abundance. The distribution of wetland mean chl *a* concentrations was unimodal, skewed right, and lacked evidence of discontinuity. Chl *a* concentration was positively correlated with the percent of the wetland basin filled by surface water ($\hat{\beta}$ = 0.0090 ±0.0018 SE) and negatively correlated with the percent of surrounding upland that was grassland ($\hat{\beta}$ = -0.6415 ±0.1993 SE). My evaluation did not support predictions of the alternative stable state hypothesis. Rather, my data suggest that these wetlands behave in a continuum of trophic structure, and that manifestation of trophic structure is influenced by a

continuum of perturbations. Accordingly, for the purposes of improving conservation planning, my findings suggest that a continuous model would be more useful than characterizing wetlands within the framework of "alternative stable states".

Introduction

Anthropogenic modifications within wetland landscapes can potentially have catastrophic effects on wetland trophic structure—an important construct of relationships that can be used to index biological productivity, biodiversity, and other services provided by wetlands. Modifications that alter hydrology, nutrient cycling, vegetation communities, and allow for fish to persist may lead to less desirable trophic structures within wetlands (Hanson and Butler 1994a; Carpenter et al. 1998; Sánchez-Carrillo and Álvarez-Cobelas 2001; Chapters 2–4). Chemical, physical, and biologic characteristics are often used as indicators of trophic structure in wetlands and ultimately as a measure of wetland productivity (Carlson 1977; Grue et al. 1988; Tome et al. 1995; Anteau and Afton 2008; Anteau et al. 2011). Accordingly, the capability to make landscape-scale assessments of wetland trophic structure may prove useful for managers to better assess wetland condition and understand influences of land use practices on that wetland condition.

Scheffer et al. (1993) proposed that there are two alternative stable states for shallow lakes (<3 m depth; hereafter wetlands), a clear state where primary productivity is dominated by macrophytes and a turbid state where primary productivity is dominated by phytoplankton (hereafter the "alternative stable states" hypothesis). Later, Scheffer and van Nes (2007) acknowledged various alternative states in temperate wetlands that are alternatively dominated by primary producers including: charophytes, submerged angiosperms, green algae, or cyanobacteria. However, the alternative stable states hypothesis maintains that there is

discontinuity in wetland community responses to environmental changes resulting in alternative equilibria producing multiple distinguishable trophic states (Scheffer and van Nes 2007). Within the core example of alternative stable states, macrophyte-dominated communities have food webs with higher density and diversity of invertebrates and vertebrates than those of phytoplankton-dominated wetlands (Hargeby et al. 1994; Scheffer and van Nes 2007). Consequently, clear-water wetlands generally provide more food and better foraging efficiency for waterbirds than do those dominated by phytoplankton (Anteau and Afton 2008, 2009). Abundance of clear-water wetlands with high productivity of aquatic macroinvertebrates are important habitat for many waterbirds that breed locally in the Prairie Pothole Region and for those migrating through to breed elsewhere (Batt et al. 1989; Swanson and Duebbert 1989; Anteau and Afton 2006, 2011).

According to the alternative stable state hypothesis, alternate states are shaped by stabilizing feedback mechanisms within wetland communities (Scheffer 2001). In clear-water wetlands, submerged aquatic vegetation can maintain a clear state by 1) reducing resuspension of sediments (Dieter 1990; James and Barko 1990); 2) suppressing phytoplankton through reduction of available nutrients and releasing allelochemicals; and 3) providing refuge for phytoplankton-grazing zooplankton and habitat for alternative prey for predators of phytoplankton-grazing zooplankton (Timms and Moss 1984; Scheffer et al. 1993; Hanson and Butler 1994a). In turbid-water wetlands, submerged vegetation growth is prevented by obstruction of light from high phytoplankton densities or suspended sediments (Scheffer et al. 1993). Further, fish can increase turbidity of wetlands by resuspending sediments and by preying upon zooplankton that consume phytoplankton, with cascading effects on the community of submerged vegetation and macroinvertebrates dependent on that vegetation for habitat

(Swanson and Nelson 1970; Timms and Moss 1984; Carpenter et al. 1985; Scheffer et al. 1993; Hanson and Butler 1994a, b; Zimmer et al. 2003). Communities in each state can resist against some degree of perturbation within the wetland basin or catchment, such as increased sedimentation, nutrification, change in fish density, water-level fluctuation, or climate variation (Scheffer et al. 1993; Hanson and Butler 1994a; Gunderson and Pritchard 2002; Bayley et al. 2007). However, beyond some threshold, a catastrophic regime shift may occur as the wetland enters an alternative stable state (Scheffer et al. 1993; Scheffer 2001) with consequences that affect productivity, species density, and species richness (Holling 1973; May 1977; Scheffer et al. 2001; Folke et al. 2004).

Chlorophyll *a* (chl *a*) concentrations are typically used as a proximate estimator of biomass of phytoplankton in aquatic systems (e.g., Carlson 1977; Scheffer et al. 1997; Bayley and Prather 2003; Zimmer et al. 2009). Previous investigations have used chl *a* concentration to differentiate clear from turbid wetlands in the Prairie Pothole Region of Minnesota (Zimmer et al. 2009) and in boreal wetlands of Alberta (Bayley and Prather 2003). The alternative stable states hypothesis postulates that wetlands can be characterized by either clear or turbid states, thus I predict that for this hypothesis to be supported wetland chl *a* concentrations should follow a bimodal distribution across the region. Further, evaluation of the frequency of turbid wetlands in various landscape conditions may provide insight into levels of disturbance that have potential to cause a regime shift. That information could be used to focus conservation or restoration efforts on wetlands that are sensitive to a regime shift.

Remote sensing-techniques used to estimate chl *a* concentrations make it possible to conduct landscape-scale assessment of wetland trophic structure. Successful estimation of chl *a* concentrations using Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus

(ETM+) imagery have been made in deep, large lakes and reservoirs (Brivio et al. 2001; Cheng and Lei 2001), and in shallow, smaller lakes (Tyler et al. 2006; Sass et al. 2007). Use of remote sensing techniques adapted for estimation of chl *a* in prairie wetlands can allow for a large enough sample of wetlands required to adequately evaluate the prediction of the alternative stable state hypothesis.

I evaluated the alternative stable state hypothesis within wetlands in the Prairie Pothole Region of North Dakota. To conduct a landscape-scale evaluation of the distribution of clear and turbid wetlands, I developed remote sensing techniques of chl *a* concentrations for larger semipermanent and shallow-water permanent wetlands. I remotely-sensed chl *a* concentrations in a large sample of wetlands and evaluated the distribution for evidence of bimodality that would support the prediction of alternative discrete states. I also evaluated if anthropogenic modifications within wetland catchments had a negative impact on wetland trophic structure by increasing chl *a* concentrations. I evaluated whether these land use and upland modification effects better predicted the probability of a wetland being turbid within a binomial model or alternatively, wetland chl *a* concentrations within a continuous model.

Methods

Study Area

I focused my effort to adapt remote sensing predictive methods for detection of chl *a* concentration and evaluation of the alternative stable states hypothesis on large (>10 ha) semipermanent and shallow-water permanent wetlands within the Prairie Pothole Region in North Dakota (Figure 6.1). I used a sample of 153 lacustrine semipermanent and shallow-water permanent wetlands that were previously randomly selected for purposes of a previous study (Anteau and Afton 2008; Chapter 2–5). These wetlands were known from the previous studies

to have open-water areas >120 m across. For each of these wetlands, detailed geomorphological and surface hydrology data were available and these wetlands were used to evaluate the influence of land use and upland modifications on chl *a* concentration. For development and evaluation of remote sensing methods, I selected a subsample of 23 wetlands that uniformly represented the range of chl *a* concentration found in the region. These relative concentrations were estimated from field observation and satellite imagery. I opportunistically included an additional five wetlands in the sample that had apparent high chl *a* concentration to extend the high end of the range; these wetlands were not in the original sample.

For purposes of evaluating the alternative stable state hypothesis, I further selected a larger sample of 1,000 additional wetlands to evaluate the distribution of chl *a* concentration. These wetlands were randomly selected from the National Wetlands Inventory (NWI; U.S. Fish and Wildlife Service 2003) using basin class coverage of NWI data (Cowardin et al. 1995; Reynolds et al. 1996; data provided by Habitat and Population Evaluation Team, U.S. Fish and Wildlife Service, Bismarck, ND). I allocated selection of wetlands across three physiographic regions of North Dakota, including: Missouri Coteau (34%), Northern Glaciated Plains (60%), and Red River Valley (6%; Figure 6.1). I restricted wetlands to those that were >10 ha basin area to improve probability of sufficient open-water area for remote sensing, compactness ratio >50 (i.e., basin area (m^2) / basin perimeter (m)) to eliminate wetlands too narrow for sufficient open-water area, and not engineered wetlands (e.g. holding ponds). I restricted lake basins (NWI lacustrine system) to those classified with the most permanent wetland area as littoral subsystems and to not include large lakes (<400 ha).

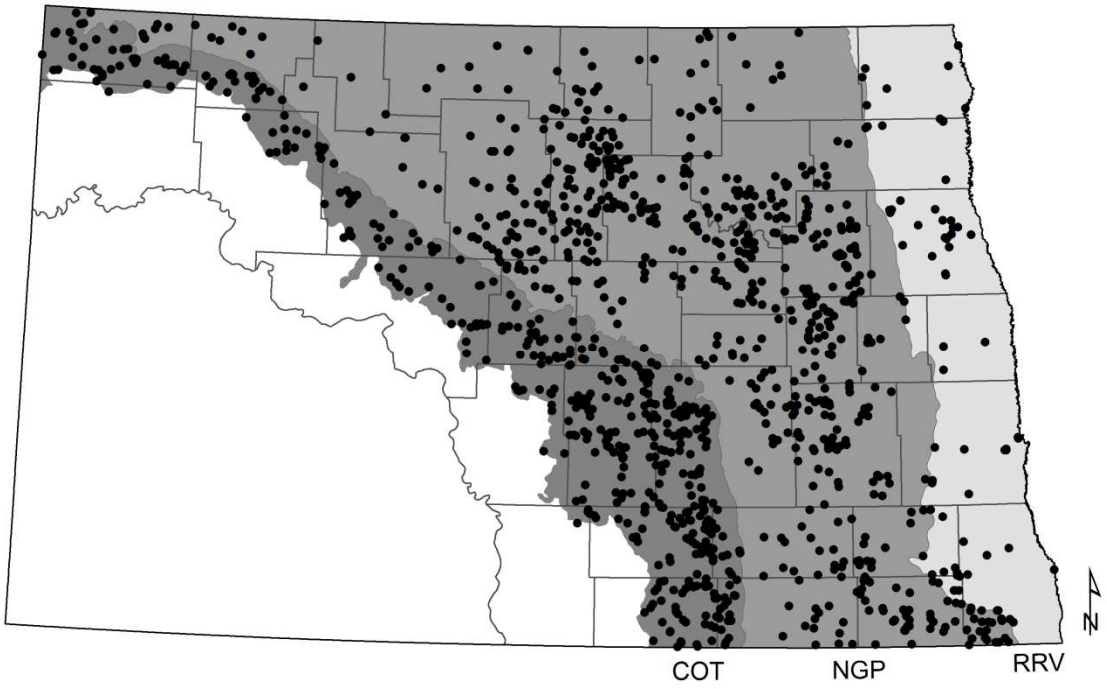

Figure 6.1. North Dakota study area showing location of semipermanent and permanent wetlands within which chlorophyll *a* concentration during 2011 was remotely-sensed. Shaded areas are three physiographic regions of the Prairie Pothole Region: Red River Valley (RRV), Northern Glaciated Plains (NGP), and Missouri Coteau (COT).

Field Data Collection

Chl *a* has traditionally been measured by collecting water samples in the field for laboratory analysis, but more recently *in situ* point sampling has been possible due to development of optical chl *a* probes (see Anteau and Afton 2008). *In situ* sampling is far less time intensive than laboratory analysis and can facilitate better spatial representation in field studies. *In situ* sampling may be less accurate than laboratory analysis; however, relevance of any field sampling is limited by the spatial extent of the sampling effort. *In situ* sampling can afford better spatial representation.

During late June through early September in 2011 or 2012, I measured chl *a* concentrations in 28 different wetlands using *in situ* sonde point sample measurements and collecting water samples for laboratory fluorometry. I expected chl *a* concentration to peak during this period of the summer, thus providing the widest range of chl *a* concentration. Estimation of phytoplankton biomass using chl *a* concentration is sensitive time of day (APHA 1998); therefore, I timed field measurements to correspond to the same time of day as Landsat satellite imagery acquisitions, approximately 10:00–14:00 CDT, and only on mostly cloud-free days no more than two days after a generally cloud-free acquisition of Landsat image. I also limited data collection to days with calm winds. I used a small boat to make measurements and collect water samples within wetlands.

In situ measurements and collected water samples were taken from open-water areas in wetlands (>30 m of open water in each direction) within 30×30 m sampling frames that were spatially aligned with pixels from either the previous TM/ETM+ image if sampling on the same day as image acquisition, or the image of interest when sampling after image acquisition. I sampled 15–25 sampling frames within each wetland, or all frames if < 25 were available. Sampling frames were arranged in clusters of five adjacent frames, and clusters were distributed to different areas within the wetland. Within each frame, I recorded *in situ* point measurements approximately at the center and 10–12 m from center in three directions (n = 4); each point sample consisted of 10 measurements collected at 1 second intervals. I collected one water sample in smaller wetlands or two samples in larger wetlands, each at the center of a sampling frame. All *in situ* measurements and water samples were georeferenced using a Trimble GeoXT (differential correction; Trimble Navigation, Sunnyvale, CA).

I used YSI 6025 chlorophyll probe and YSI 6136 turbidity probe (YSI Incorporated, Yellow Springs, Ohio) for *in situ* measurements at each sample point. At the beginning of each sampling day, I calibrated the chlorophyll probe to a zero measurement using distilled water. I also recorded measurements in 0.5 mg/L Rhoadamine WT at the beginning and end of each sampling day to check for sensor drift. I calibrated the turbidity probe once at the beginning of each season. I aggregated multiple readings from each point sample and the four point samples within the sampling frame to calculate a median value for chlorophyll and turbidity. Use of the median (rather than the mean) value better controls for erroneous readings that occur periodically in electronic-probe measurements.

I collected water samples that corresponded directly to the georeferenced *in situ* location to enable post-calibration of the probe using results from laboratory fluorometric analysis of chl *a*. Each water sample consisted of 1 L of water collected just below the surface. Water samples were filtered through a glass fiber filter (45 µm, 47 mm diameter). Filters were immediately frozen for fluorometry analysis (APHA 1998) within 10 days of collection. Laboratory analysis was performed by North Dakota Department of Health's Surface Water Quality Management Program. I used regression analysis without an intercept to calibrate *in situ* chl *a* measurements to laboratory fluorometry results.

Landsat Data

I obtained Landsat 5 TM and Landsat 7 ETM+ product level 1T precision and terrain corrected images from Earth Explorer (U.S. Geological Survey 2014). A total of 19 images of the study area were used from scenes within path 29–35 and row 26–28 of the Worldwide Reference System 2 (Table 6.1). All images used were <12% cloud cover, with the exception of two images with 18% and 45% cloud cover from which only cloud-free portions of the image

were used to correspond to cloud-free field data collection. I converted image digital numbers to top-of-atmospheric reflectance using at-sensor values (Chander et al. 2009), and then I used the Automated Cloud-Cover Assessment algorithm to detected and masked clouds (Irish et al. 2006). I corrected images for atmospheric effects using the 6S algorithm (Vermote et al. 1997) with optical depth from the Moderate Resolution Imaging Spectroradiometer (MODIS) Level 3 Daily Atmosphere Gridded Product (NASA 2014). For each scene, I calculated the optical depth as the scene average of mean optical land and ocean values from the MODIS product.

I extracted reflectance values (R) for TM/ETM+ bands 1–5 and 7 (Table 6.2) from pixels that corresponded to *in situ* measurement sample frames or open-water pixels from the 1,000 wetlands. I used images acquired between 3 July and 5 September of 2011 with preference for cloud-free images nearest 19 July (ordinal day 200). To select open-water pixels within the 1,000 randomly selected wetlands, I initially offset (i.e., buffered) the perimeter of the NWI basin class coverage polygon 60 m toward the center of the wetland. I then applied a series of filters to eliminate pixels that were not registering as open-water using band 5 ($R_{B5} > 0.03$), registering apparent emergent or submerged vegetation ($R_{B4} / R_{B2} \geq 2$), or had a signature of a hypersaline turbid water wetland ($R_{B1} > 0.05$). Hypersaline wetlands were excluded from this analysis because their water quality condition is beyond the scope of this analysis, and their overall brightness within the spectral signature present problems remotely-sensing a chl *a* signature. From the initial 153 wetland sample combined with the additional 1,000 randomly selected wetlands, 978 wetlands were suitable for remote sensing of chl *a* concentration after open-water pixel filters were applied (>1 open-water pixel).

Table 6.1. Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) scenes used to build and evaluate a predictive model of Chlorophyll *a* concentration in wetlands (Model) and to make predictions within wetlands in a landscape-scale assessment (Predict). Listed are the Landsat Scene Identifier, year of image (Year), ordinal day of year (Day), World Reference System 2 scene (Row and Path), and optical sensor that acquire the image (Sensor).

Scene Identifier	Year	Day	Path	Row	Sensor	Model	Predict
LT50330262011184PAC01	2011	184	33	26	TM	Yes	No
LT50330272011184PAC01	2011	184	33	27	TM	Yes	Yes
LT50310272011186PAC01	2011	186	31	27	TM	Yes	Yes
LT50310282011186PAC01	2011	186	31	28	TM	No	Yes
LT50320262011193PAC01	2011	193	32	26	TM	No	Yes
LT50320272011193PAC01	2011	193	32	27	TM	Yes	Yes
LT50310262011202PAC01	2011	202	31	26	TM	No	Yes
LT50300262011211PAC01	2011	211	30	26	TM	No	Yes
LT50300272011211PAC01	2011	211	30	27	TM	Yes	Yes
LT50300282011211PAC01	2011	211	30	28	TM	No	Yes
LT50320262011225PAC01	2011	225	32	26	TM	No	Yes
LT50350262011230PAC01	2011	230	35	26	TM	No	Yes
LT50290282011236PAC03	2011	236	29	28	TM	No	Yes
LT50340262011239PAC01	2011	239	34	26	TM	No	Yes
LT50330262011248PAC01	2011	248	33	26	TM	No	Yes
LE70300282012174EDC00	2012	174	30	28	ETM+	Yes	No
LE70300282012190EDC00	2012	190	30	28	ETM+	Yes	No
LE70300272012222EDC00	2012	222	30	27	ETM+	Yes	No
LE70310282012229EDC00	2012	229	31	28	ETM+	Yes	No

Table 6.2. Spectral resolution (μm) for each band of Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) imagery used to develop a remote sensing equation for Chlorophyll *a* concentration. Band 6 (thermal) was not used. Data are courtesy of U.S. Geological Survey (http://landsat.usgs.gov/).

Landsat	TM	ETM+
Band 1	0.45–0.52	0.45–0.52
Band 2	0.52–0.60	0.52–0.60
Band 3	0.63–0.69	0.63–0.69
Band 4	0.76–0.90	0.77–0.90
Band 5	1.55–1.75	1.55–1.75
Band 7	2.08–2.35	2.09–2.35

Landscape Data

I assembled wetland geomorphological characteristics and land cover/land use from uplands surrounding each of the 153 wetlands in the initial sample for which I was able to predict chl *a* concentrations in 2011 using TM. I used catchment area, percent of wetland drainage within catchment, percent wetland filled its topographic basin, and water surface area rate of change from Chapter 2 (also see McCauley et al. In Review). I characterized upland land use by using the percent of the catchment that was cropland estimated by photointerpretation (McCauley et al. In Review; Chapter 2). Additionally, I summarized percent of upland within 400 m and 800 m of each wetland during 2011 that was crop, grass, and specifically corn or soybeans using the Cropland Data Layer (CDL; NASS 2011). I evaluated CDL as a measure of land cover/land use at fixed distances because the photointerpretation method using defined catchments was labor intensive and would not be practical on a larger sample of wetlands. Accordingly, I created seven different measures of land cover/land use to evaluate.

Wetland Surface Area Dynamics

I included water dynamics in my analysis evaluating influence of land use and upland modifications on wetland chl *a* concentrations because vegetation communities can be influenced by wetland water dynamics (Weller and Spatcher 1965; van der Valk and Davis 1978). In Chapter 2, I defined wetland water surface area dynamics within the variable climate conditions during 2003–2010 in terms of rate of decrease during a drying phase and rate of increase during a wetting phase. I calculated these rates using the maximum surface area during the wet periods and minimum surface are during the dry period within the equation:

$$ln\left(\frac{\text{Surface Area}_{\text{final}}}{\text{Surface Area}_{\text{initial}}}\right)$$

Statistical Analysis

Post-calibration of in situ *chlorophyll* a

I tested the importance of turbidity within the regression model as a covariate to account for potential differences between *in situ* and filtered laboratory samples. I evaluated collinearity between chl $a_{in\ situ}$ and turbidity using variance inflation factor (vif = 2.31). I used the final regression equation to calculate post-calibrate chl *a* (chl a_{pc}) values for all *in situ* measurements (R Development Core Team 2010).

Landsat to predict in situ *chlorophyll* a

For development of a model to predict wetland chl *a* concentration using TM/ETM+ data I used *in situ* sampling frames corresponding to image pixels as the observational unit. I randomly split *in situ* sampling frames into two halves equal in number to create a model development data set and a model evaluation data set. I split sampling frames into development and evaluation groups rather than individual wetlands because I was only able to sample 26 wetlands. I evaluated previously published (see list in Sass et al. 2007) and new combinations of

single bands, multiple band combinations, and principal components of visual spectrum bands (1–3) and all non-thermal bands (1–5, 7) in regression analysis as predictor variables of chl a_{pc} (ln). I excluded predictor variables with strong collinearity ($r \geq 0.40$) to others in the same model. I used 95% confidence intervals to evaluate importance of predictor variables and model R^2 values to compare goodness-of-fit among models and to select the best model for making predictions. I then used the best model to make predictions (chl a_{rs}) within *in situ* sampling frames from the evaluation data set. I evaluated regression coefficients and correlation to determine adequacy of chl a_{rs} as a predictor of chl a_{pc}. Finally, I evaluated prediction performance at a wetland resolution by regressing wetland mean chl a_{pc} on wetland mean chl a_{rs}.

Landscape distribution of wetland chlorophyll* a *concentration

I used the chl a_{rs} predictive equation to estimate chl *a* concentration in 978 randomly selected wetlands at one point in time during 2011. I applied the equation to open-water pixels from TM images, and then calculated the wetland mean chl a_{rs}. I evaluated whether the distribution of chl *a* concentrations in wetlands supported the alternative stable states hypothesis by plotting a histogram of wetland mean chl a_{rs} concentrations. Interpretation of distributions by categorical frequency is sensitive to selection of category break points and bin ranges. Clearly, to evaluate bimodality a uniform bin size is needed. I used 5 $\mu g\ L^{-1}$ bins to represent wetland chl *a* concentrations. A distinct bimodal distribution would support predictions made under the hypothesis of clear and turbid wetlands, measurable by chl *a*.

Landscape factors influencing chlorophyll* a *concentration

I quantitatively assessed two models for evaluating influences of land use and upland modifications on trophic structure. The first was an alternative stable state model that examined the probability of a wetland being in a turbid or clear state (as defined by Bayley and Prather

2003; Zimmer et al. 2009) using a binomial distribution. Second, represented an alternative research hypothesis where trophic status changes continuously with changes in landscape variables. For that model a continuous distribution of wetland chl *a* concentration was used. In the prediction following the alternative stable state hypothesis, landscape variables should better predict the probability of a wetland being turbid within a binomial distribution than would landscape variables predict wetland chl *a* concentration within a continuous distribution. Within the initial sample of wetlands for which detailed geomorphological and surface hydrology data were available, 117 wetlands were suitable for remote sensing of chl *a*. I used chl a_{rs} derived from TM data collected in 2011 as the response variable in continuous regression analysis and classified chl a_{rs} >20 μg L^{-1} as a turbid wetland in logistic regression analysis (R Development Core Team 2010). For each analysis I used the same *a priori* model that included land use and upland modification predictor variables from wetland for which I had detailed geomorphological and surface hydrology data. Predictors included: wetland basin percent full, percent catchment area that was drained wetland, catchment area (*ln*), water surface area dynamics, and land cover/land use. Prior to fitting my *a priori* model, evaluated drying rate versus wetting rate as a measure of water surface area and seven different measures of land use/land cover by iteratively fitting each one with all other predictor variables of the *a priori* model. I repeated this process for both the binomial and continuous models. I selected the model with the greatest R^2. I determined predictor variables to be important in the model if 95% confidence intervals of parameter estimates did not overlap zero. I plotted fitted values versus response values for both the binomial model and continuous model (one point omitted at [21,132]). I compared R^2 to evaluate which model distribution was better supported by my data.

Results

Post-Calibration of *In Situ* Chlorophyll *a*

I recorded 1876 *in situ* point samples and collected 45 water samples within 28 wetlands. *In situ* chl *a* measurements predicted laboratory fluorometry values well (R^2 = 0.93, $F_{2, 43}$ = 284.9) provided that the level of turbidity was in the model:

$$\text{Chl } a_{\text{Lab}} = 0.47[\pm 0.18 \text{ SE}](\text{Chl } a_{in\ situ}) + 2.90\ [\pm 0.21 \text{ SE}](\text{turbidity})$$

Landsat to Predict *In Situ* Chlorophyll *a*

The best models to predict chl *a* concentration in wetlands using TM and ETM+ were:

$$ln(\text{Chl } a_{\text{rs TM}}) = 6.70 + 9.27 \left(\frac{R_{B3} - R_{B5} - R_{B7}}{\sqrt{R_{B3} + R_{B5} + R_{B7}}}\right) - 0.74 \left(\sqrt{R_{B4}^{-1}}\right)$$

$$ln(\text{Chl } a_{\text{rs ETM+}}) = 6.87 + 17.95 \left(\frac{R_{B3} - R_{B5} - R_{B7}}{\sqrt{R_{B3} + R_{B5} + R_{B7}}}\right) - 0.74 \left(\sqrt{R_{B4}^{-1}}\right)$$

Each parameter in the model was important for prediction (Table 6.3). Chl a_{rs} described 72% (R^2; $F_{4, 311}$ = 197.2) of the variability within *in situ* chl a_{pc} values. In the evaluation data set, chl a_{rs} predicted *in situ* chl a_{pc} values with an intercept of 3.970 (SE = 3.353) and slope of 1.269(SE = 0.048), with an R^2 of 69% ($F_{1, 314}$ = 693.9). Aggregated mean chl a_{rs} and *in situ* chl a_{pc} values in 26 wetlands were highly correlated (r = 0.93, t = 3.733, df = 24, P = 0.005; Figure 6.2).

Landscape Distribution of Wetland Chlorophyll *a* Concentration

Chl a_{rs} ranged 3–714 μg L^{-1}, with a mean of 27 μg L^{-1} and median of 17 μg L^{-1}. The distribution of wetland mean chl *a* concentration was skewed right (Figure 6.3), and no evidence of bimodality was present in a histogram of truncated at 100 μg chl *a* L^{-1} (Figure 6.4).

Landscape Factors Influencing Chlorophyll *a* Concentration

Chl a_{rs} ranged 4–133 μg L^{-1}, with a mean of 19 μg L^{-1} and median of 15 μg L^{-1}. In the *a priori* model describing the influence of land use and upland modifications on wetland chl *a*

concentration the measures that best fit the data, for those parameters that had multiple measures, were rate of water surface area rate of decrease during the drying phase and CDL derived percent grassland within 400 m of the wetland (Table 6.4). These two predictor variables were used in addition to wetland basin percent full, percent catchment area that was drained wetland, and wetland catchment area (*ln*). The binomial model with the same variables was ranked second best, but model fit was essentially not different from the top ranked model (Table 6.4). The continuous model accounted for nearly twice the amount of variability in trophic structure (R^2 = 0.32, $F_{5, 111}$ = 10.61; Figure 6.5A) than the binomial model (R^2 = 0.19, $\chi^2_{df=5}$ = 26.33; Figure 6.5B). Wetland basin percent full was positively correlated with chl *a* concentration, and percent upland that was grassland was negatively correlated with chl *a* concentration (Table 6.5). There was not sufficient evidence for correlation of any of the other predictor variables with chl *a* concentration (Table 6.5).

Table 6.3. Regression parameter estimates from a model developed to detect chlorophyll *a* concentrations (*ln*) within semipermanent and permanent wetlands using Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus image data. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits. At-surface-reflectance values corrected for atmospheric effects ($R_{band\ \#}$) were used to develop the model. Predictor $X_1 = (R_3 - R_5 - R_7) / (R_3 + R_5 + R_7)^{0.5}$ and $X_2 = R_4^{-0.5}$. A colon indicates an interaction predictor term.

Predictor	$\hat{\beta}$	SE	LCL	UCL
Intercept	6.869	0.193	6.491	7.247
X_1	17.948	1.493	15.022	20.873
X_2	-0.740	0.032	-0.803	-0.676
Sensor $_{TM}$	-0.174	0.081	-0.334	-0.015
X_1:Sensor $_{TM}$	-8.675	1.627	-11.863	-5.486

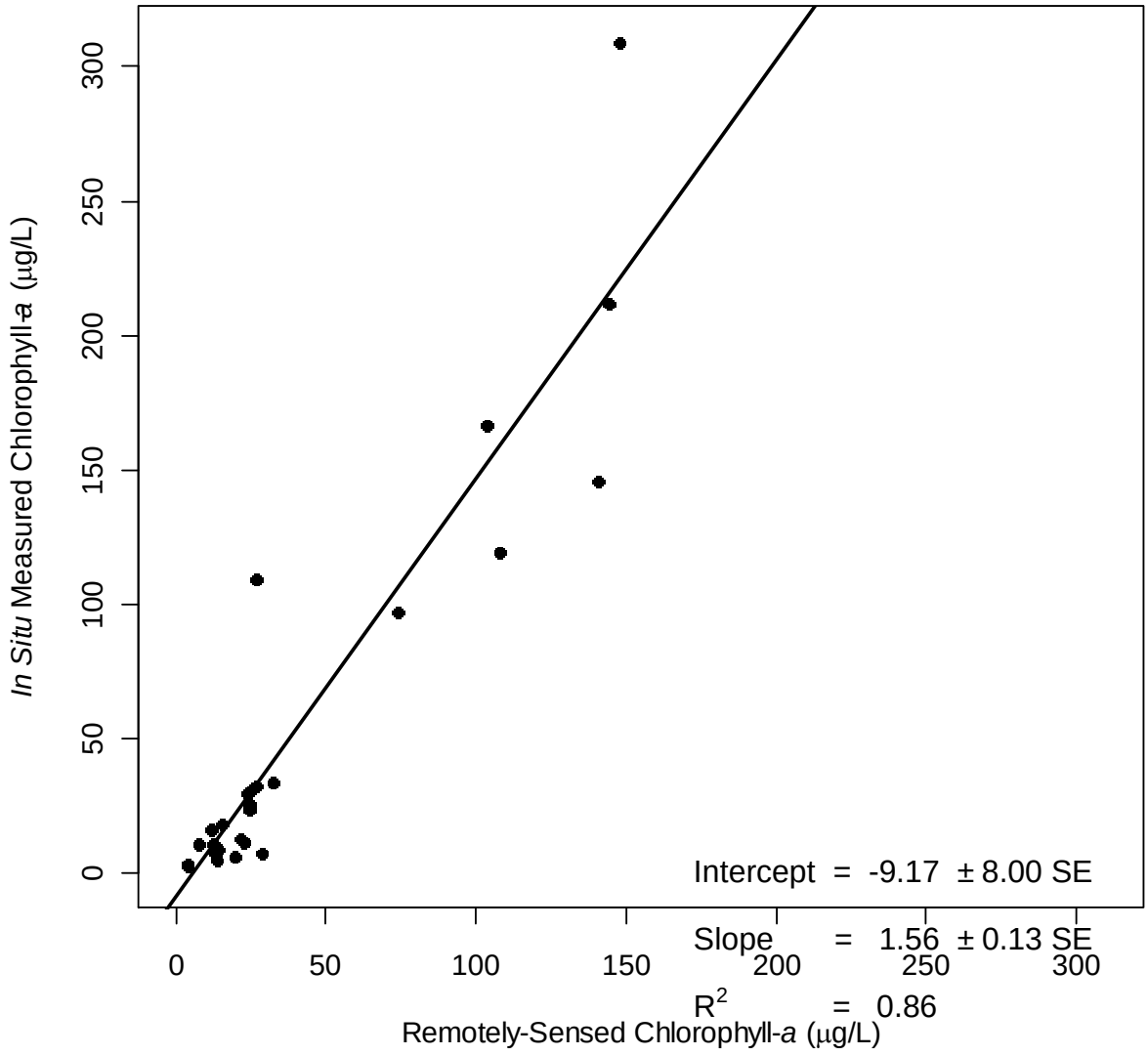

Figure 6.2. Accuracy evaluation of remotely-sensed chlorophyll *a* concentrations to predict mean *in situ* measurements within 26 semipermanent and permanent wetlands in North Dakota.

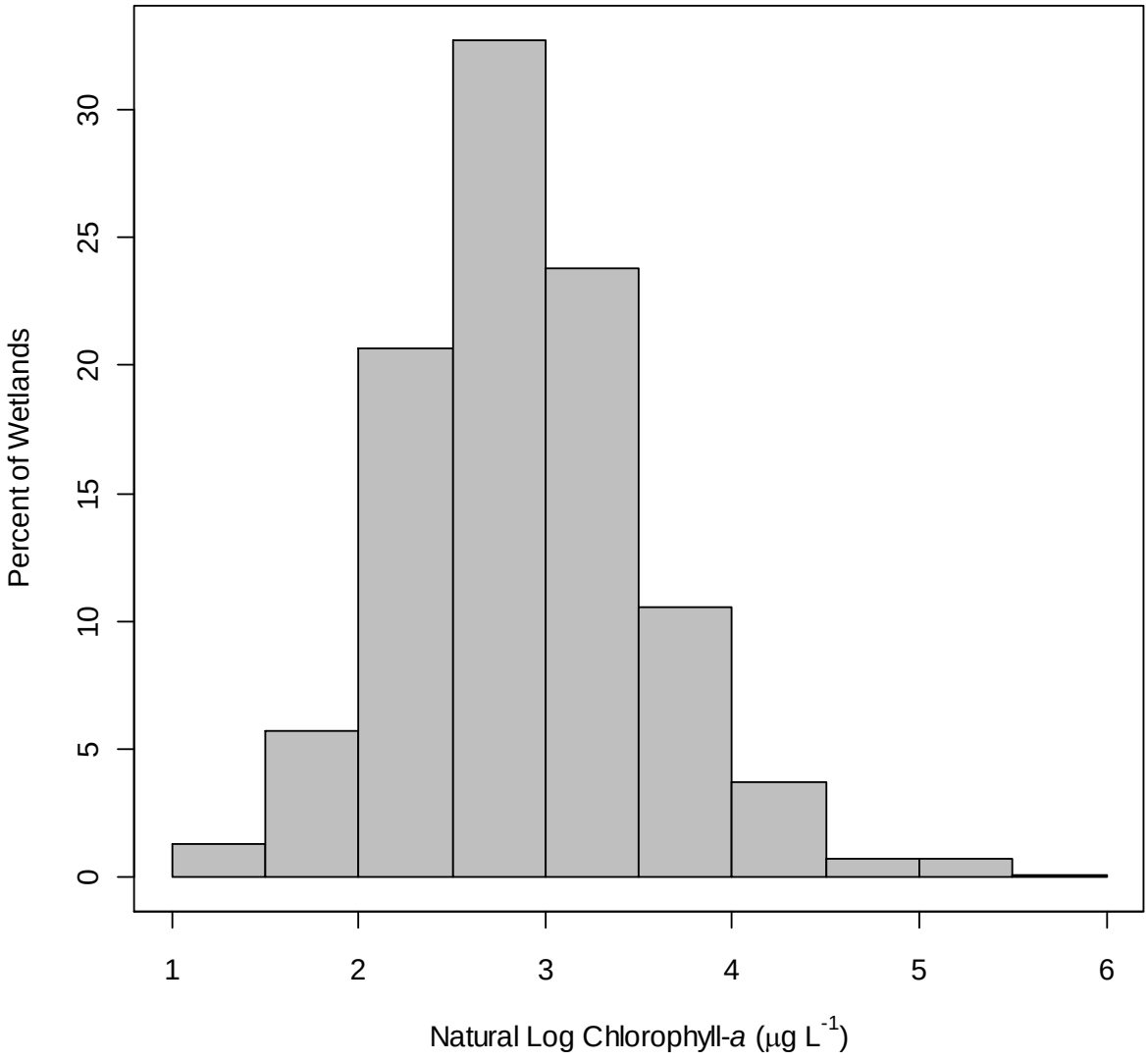

Figure 6.3. Natural log distribution of remotely-sensed chlorophyll *a* concentrations within 978 randomly selected semipermanent and permanent wetlands in North Dakota.

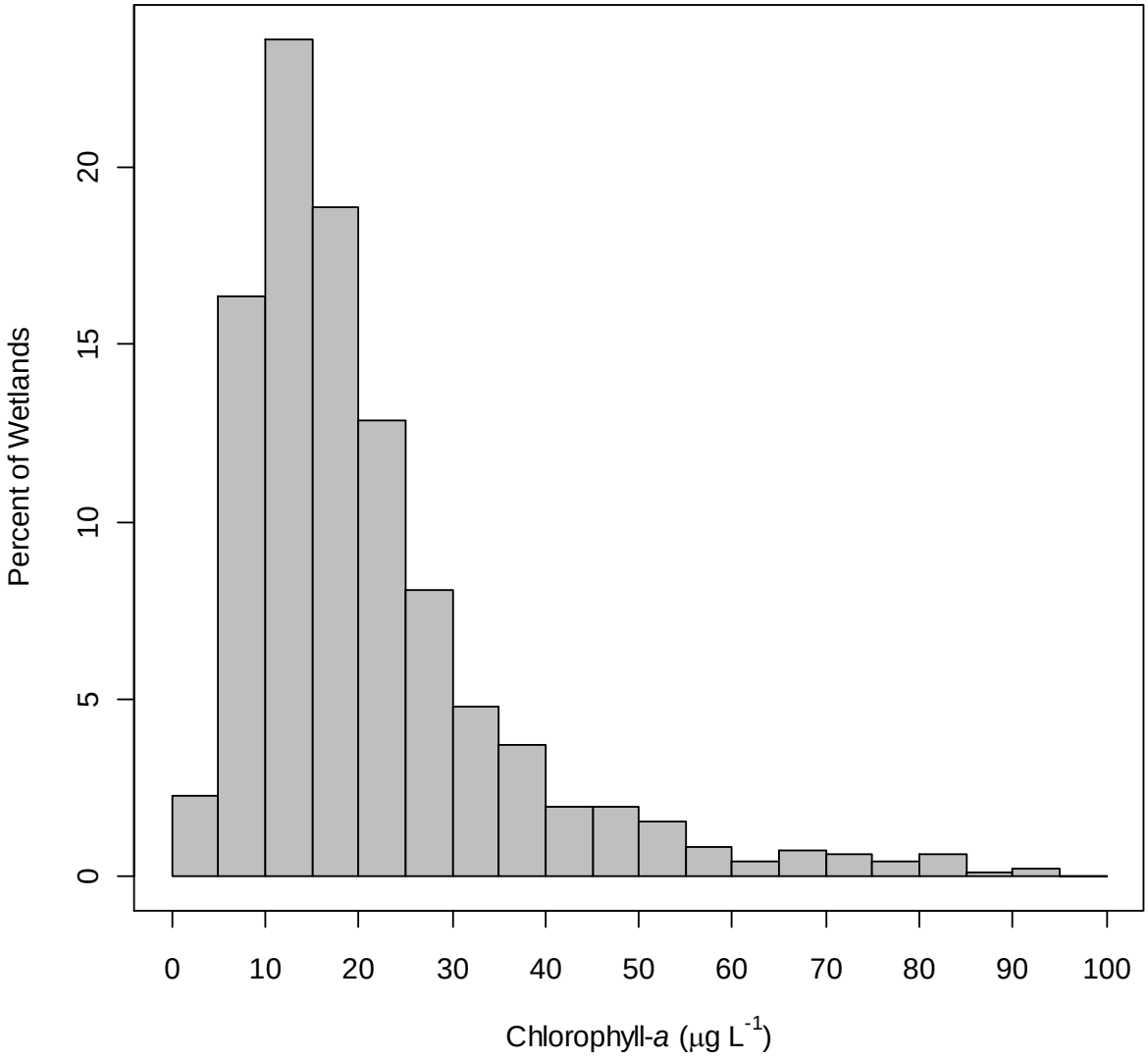

Figure 6.4. Distribution of remotely-sensed chlorophyll *a* concentrations within 965 of 978 randomly selected semipermanent and permanent wetlands in North Dakota. Histogram truncated at 100 μg L^{-1}.

Table 6.4. Comparison of coefficient of determination (R^2) from regression analysis of two alternative *a priori* models used to evaluate the influence of land use and upland modifications on probability of a wetland being in a turbid state using a binomial distribution (Model 1) or concentration of Chlorophyll *a* within wetlands using a continuous distribution (Model 2). Water surface area change during alternative climatic phases (Phase) and measures of land use/land cover (LU/LC) were used in addition to wetland basin percent full, percent catchment area that was drained wetland, and wetland catchment area (*ln*). See text for details.

Phase	LU/LC	Model 1: R^2	Model 2: R^2
Drying	Grassland: 400 m	0.201	0.323
Drying	Grassland: 800 m	0.195	0.322
Wetting	Grassland: 400 m	0.205	0.320
Wetting	Grassland: 800 m	0.200	0.319
Drying	Cropland: 400 m	0.166	0.272
Drying	Cropland: 800 m	0.160	0.268
Wetting	Cropland: 400 m	0.168	0.265
Drying	Corn & Soy: 800 m	0.147	0.262
Drying	Corn & Soy: 400 m	0.148	0.262
Drying	Cropland: Catchment	0.145	0.262
Wetting	Cropland: 800 m	0.162	0.260
Wetting	Corn & Soy: 800 m	0.147	0.253
Wetting	Corn & Soy: 400 m	0.148	0.252
Wetting	Cropland: Catchment	0.143	0.249

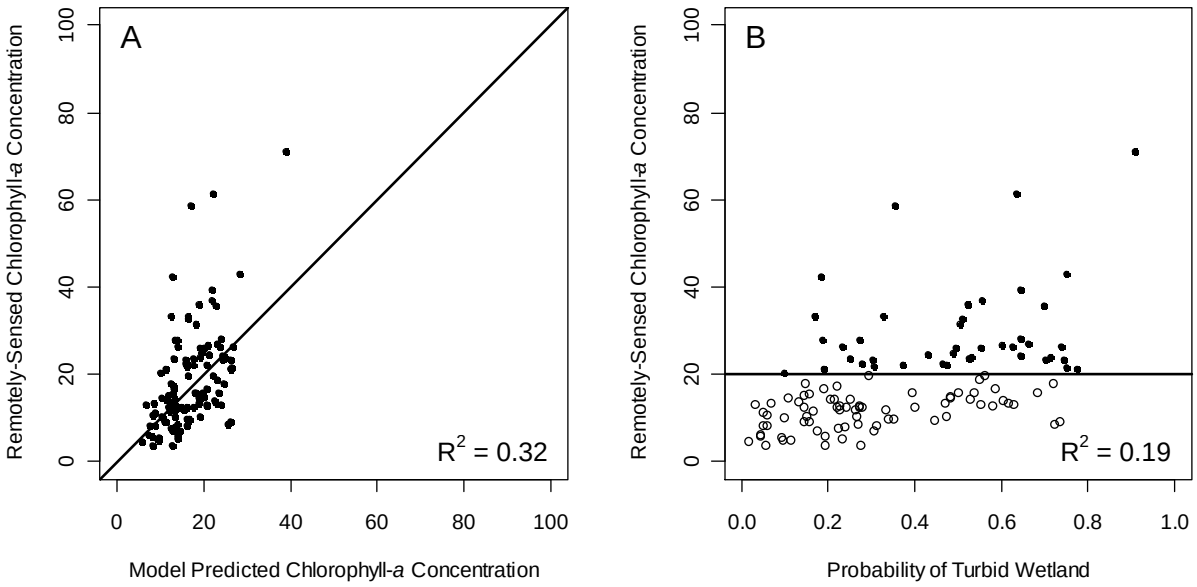

Figure 6.5. Remotely-sensed chlorophyll *a* concentrations versus fitted values from alternative models using influence of land use and upland modifications to predict A) wetland chlorophyll *a* concentrations modeled in a continuous distribution, and B) probability of a wetland being turbid (>20 μg L^{-1}). The diagonal line in A is a 1:1 relationship, and the horizontal line in B separates wetlands classified as clear-water wetlands (open circles) from turbid-water wetlands (filled circles) classified using a threshold of >20 μg L^{-1}.

Table 6.5. Regression parameter estimates from a model used to evaluate the influence of land use and upland modifications on chlorophyll *a* concentrations (*ln*) within 110 semipermanent and permanent. Included are: estimated coefficients ($\hat{\beta}$), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits.

Predictor	$\hat{\beta}$	SE	LCL	UCL
Intercept	2.223	0.259	1.716	2.730
Basin Full	0.009	0.002	0.005	0.013
Catchment Drainage	-0.002	0.019	-0.039	0.034
Drying Dynamic	0.201	0.155	-0.103	0.506
Grassland	-0.642	0.199	-1.032	-0.251
Catchment Area (*ln*)	0.043	0.029	-0.015	0.101

Discussion

In accordance with the alternative stable states hypothesis, I predicted that wetland chl *a* concentration across the Prairie Pothole Region in North Dakota would follow a bimodal distribution. However, my results did not provide support for that prediction, but rather I found chl *a* concentrations exhibited a continuous, right-skewed distribution. Previous investigations have used chl *a* concentration to differentiated clear from turbid wetlands in the Prairie Pothole Region in Minnesota using <22 $\mu g\ L^{-1}$ as clear lakes and >31 $\mu g\ L^{-1}$ as turbid lakes (Zimmer et al. 2009; n= 72) and in boreal wetlands in Alberta where a threshold of 18 $\mu g\ L^{-1}$ differentiate clear from turbid (Bayley et al. 2007; n = 112). Earlier, Bayley and Prather (2003) found that 62% of 148 boreal wetlands in Alberta were in a typical clear state with a high density of submerged aquatic vegetation and low chl *a* concentration, or in a turbid state with high chl *a* and low density of submerged aquatic vegetation; while, the remaining 38% of wetlands were either high or low in both density of submerged aquatic vegetation and chl *a* concentration. If

alternative states do exist, separation between the modes of each state should be more distinct in a larger sample across landscapes within a region. Yet, I found more evidence to support a continuous distribution.

There are alternative explanations as to why a continuous rather than bimodal distribution better describes wetland chl *a* concentration evaluated across landscapes within the Prairie Pothole Region. If state-change control points are driven by climate, chemical constituents, nutrients, depth and wetland size (Scheffer and van Nes 2007), then heterogeneity among driving factors increases the variation in those control points such that manifestation of each state can vary from wetland to wetland. Accordingly, indicators of alternative states (e.g., chl *a* concentrations) may vary among wetlands enough to appear continuously distributed. Individual wetlands may indeed exhibit individual states, but among a large sample of wetlands across landscapes the expected bimodal distribution of a state indicator for a single wetland could be masked. Time-series analyses of chl *a* concentration within wetlands that are selected at random across landscapes within the region might provide evidence to support this explanation. However, if individual wetlands have different state-change control points that also lead to clear versus turbid states defined at different chl *a* concentrations, the alternative stable state hypothesis might not be useful for conservation planning at a landscape scale.

A second alternative explanation considers continuous changes in biological communities and the potential for less abrupt transitions in trophic structure. This explanation is not in line with the alternative stable states hypothesis, but rather proposes that trophic structure in prairie wetlands is better explained within a continuum. Changes in dominant species of algae, plants, and animals can occur gradually within wetland communities suggesting trophic structure may change continuously at various rates (Scheffer et al. 1994; Van den Berg et al.

1999; Scheffer and van Nes 2007) rather than the abrupt or catastrophic changes illustrated in some of the case-study wetlands. Certainly, catastrophic state changes as a result of reduced nutrient inputs, biomanipulations, or winter-kill events have been documented by other investigators (Scheffer et al. 1993; Hanson and Butler 1994a; Bayley et al. 2007; Hobbs et al. 2012). However, those cases were also the result of marked changes in stressors affecting those wetlands. It is not clear if a catastrophic regime shift would have been observed if the change in stressors were more gradual. More-abrupt changes in wetland trophic structure would be expected to result from more-abrupt events such as biomanipulation which is essentially a biological perturbation (Carpenter et al. 1985). Conversely, more physical perturbations like increased sedimentation or changes in hydrology might actually produce more-gradual changes in wetland community structure rather than the catastrophic changes predicted by the alternative stable state hypothesis. Thus, a continuum of wetland communities might better describe wetlands across these particular landscapes, rather than two distinctive, alternative states (van der Valk 1981; Euliss et al. 2004). Further, the myriad physical and chemical factors that influence biological communities in prairie wetlands (Weller and Spatcher 1965; Stewart and Kantrud 1972; van der Valk and Davis 1978; Euliss et al. 2004) have created more variety of wetland conditions, trophic structures, and levels of biological productivity in prairie wetlands than can be described by discrete states.

Distinguishing between biological, chemical, and physical perturbations might be useful not only to determine rates of wetland community change, but potentially to understand potential future wetland conditions or states (Euliss et al. 2004; Hanson et al. 2005). Shallow lakes have been observed to alternate between states, returning to same state after biological state-changing perturbations (Scheffer et al. 1993; Hobbs et al. 2012). However, if more physical disturbances

on adjacent uplands cause a change to the physical structure of the wetland system, a more-permanent change could prevent a wetland from returning to a prior state. Two examples of disturbances commonly imposed on wetlands in the Prairie Pothole Region are tillage of adjacent uplands that increases sedimentation rates (Gleason and Euliss 1998) and drainage of smaller wetlands to consolidate water into larger wetland basins (Anteau 2012; McCauley et al. In Review; Chapter 2). Each of these perturbations could change the physical structure of the wetland by altering wetland depth and consequently the wetland community.

Consolidation drainage can unbalance hydrologic dynamics (Chapter 2), resulting in higher and more-stable water levels. Expanded wetland connectivity produced by higher water levels can reduce basin isolation. Creation of more corridors for fish colonization will increase the occurrence of sustained fish populations (Chapter 4), subsequently increasing turbidity in fish-populated wetlands (Hanson et al. 2005). Fish occurrence in my study wetlands was not independent of landscape modifications that altered wetland physical structure (Chapter 2–4); therefore, I did not include "fish" among landscape variables in the model to explain chl *a* concentrations. Colonization of fish into clear-water wetlands represents a biological perturbation and changes in biological communities are often abrupt, reflecting catastrophic changes in trophic structure (Carpenter et al. 1985; Scheffer 2001; Zimmer et al. 2003; Zimmer et al. 2006). However, a model that uses landscape variables that are more-readily available than are fish data (e.g., land use/land cover, hydrogeomorphology, and water levels) is likely more useful for landscape- or regional-scale assessment of wetland condition and is more aligned with practical conservation efforts.

Prairie wetland communities are typically regulated by fluctuation of water levels driven by climate variability. These fluctuations likely maintain wetlands on the clearer side of the

continuum through elimination of fish and by improving growth conditions for submerged aquatic vegetation. If disturbances like consolidation drainage reduce or eliminate the drawdown portion of the cycle, then wetlands may become more turbid as these wetlands likely receive more sediment and nutrients and are more likely to maintain a fish community. Alternatively, water drawdowns in a turbid wetland could trigger a shift toward clearer-water through the elimination of fish (Blindow et al. 1993; Bayley et al. 2007) and establishment of submerged aquatic vegetation in the shallower water. Within a disturbed prairie landscape dominated by turbid, water-stabilized wetlands, restoration of more-dynamic hydrology is likely a prerequisite to the recovery of clear-water biological communities.

Grassland surrounding a wetland was an important predictor of chl *a* concentration in my analysis. Relative to wetlands that are surrounded by grassland or that have little or no adjacent cropland, wetlands surrounded by a high proportion of cropland likely receive significant amounts of sediment delivered by wind and runoff water, and thus tend to be more turbid (Gleason and Euliss 1998). Agricultural practices that have put more land into production have increased the amount of exposed soil on the landscape (see Euliss et al. 2010). Sedimentation has been identified as the leading pollutant in prairie wetlands, reducing the abundance of submerged aquatic vegetation (USEPA 1995; Gleason and Euliss 1998). Furthermore, run-off water and sediments can transport nutrients, salts and agricultural chemicals from fields to wetlands, changing the chemical condition of the wetland (Neely and Baker 1989), potentially increasing phytoplankton blooms, and increasing the probability of a wetland being turbid.

As a technical note, turbidity resulting from suspended sediments can affect *in situ* measurements of chl *a* concentration. I found that controlling for turbidity measured by an optical probe was essential to post-calibrate optical probe chlorophyll measurements to results

from laboratory assessment of chl *a* via fluorometry. Most large-particle constituents of turbidity are filtered out of samples prior to laboratory fluorometry. Any optical sensor is likewise affected by all sources of turbidity while making *in situ* measurements; therefore, turbidity likely imposes variability in remotely-sensed chl *a* concentrations. I used a novel approach to account for turbidity by incorporating near infrared (band 4) and short-wave infrared reflectance (bands 5 and 7) accounted for some of the variation associated with turbidity not due to chl *a* (Moore et al. 1999; Schalles 2006; Gilerson et al. 2010). Near infrared and short-wave infrared wavelengths are mostly absorbed in clear water, but suspended solids in water will backscatter these wavelengths increasing reflectance values in turbid water (Moore et al. 1999; Schalles 2006; Gilerson et al. 2010). There is potential for further investigation to refine remote sensing algorithms to better understand spectral signatures of wetland water types and vegetation communities.

If alternative states do exist and can be defined in individual wetlands, understanding regime-shift triggers and the resilience of biotic communities could allow managers to more effectively manipulate wetland states where more detailed information is available on prior perturbations and other drivers of biological communities. However, wetland chl *a* concentrations resemble a continuous distribution across landscapes in the Prairie Pothole Region of North Dakota. This, plus the fact that landscape variables better predict chl *a* concentration as a continuous, not a binomial, distribution suggests that the alternative stables states hypothesis might not be an appropriate framework for assessing processes relevant to conservation of wetlands across the prairie landscapes. Accordingly, for the purposes of improving conservation delivery and planning, I question the usefulness of characterizing wetlands within an alternative stable state framework. Alternatively, evaluation of wetland

condition at a larger scale might best focus on simply evaluating patterns of anthropogenic disturbances that correspond to degradation of wetland biological communities and their ecological functions.

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CHAPTER 7. GENERAL CONCLUSION

Waterbird conservation can benefit from evaluation of wetland habitat within watershed-derived wetland complexes in the Prairie Pothole Region. These larger-than-wetland-scale evaluations provide insight into processes that drive changes within remaining wetlands and provide context to trends that may be important for understanding waterbird populations in the region (Niemuth et al. 2009). Migrating and breeding waterbirds use complexes of wetlands during each life stage (Skagen and Knopf 1994; Niemuth et al. 2006). Therefore, conservation efforts need to be based on how wetland habitat availability is affected by landscape changes that result from anthropogenic disturbances (Higgins et al. 2002), all in a temporal context of climate variability and longer-term climate change (Johnson et al. 2010; Niemuth et al. 2010; Loesch et al. 2012).

Identification of the implications that anthropogenic disturbances have on waterbird habitat at landscape and regional scales can help prioritize effective conservation efforts. I found that consolidation drainage has a progressive-chronic effect on the hydrology of more-permanent wetlands by increasing the amount of surface water these wetlands receive, at a rate exceeding their rate of water loss (Chapter 2). Thus, these wetlands increase in size until they fill their topographic basin. Further, I speculated that wetlands occupying topographic basins that are already full will spill additional drainage water to downstream watersheds, adding to regional flood problems. In extensively drained catchments there are fewer small wetlands to provide waterbird habitat, while productivity of remaining larger wetlands has been adversely affected (Chapters 3–5). Drastic disturbances to natural wetland complexes, composed of wetlands having various hydroperiods, have likely degraded overall landscape productivity of waterbird food resources across wet–dry climate periods. This process has produced a landscape

increasingly composed of wetlands representing two extremes: drained former-wetland basins and permanent lakes. This altered landscape is likely less able to provide necessary migration and breeding habitat for waterbirds due to reduced productivity of essential plant and animal forage (Afton and Anderson 2001; Anteau et al. 2011). In addition, structural changes to wetlands may reduce the abundance of foraging habitat, especially for shorebirds (Niemuth et al. 2006; Anteau 2012).

Altered hydrology can change wetland communities and result in less biodiversity dominated by less-desirable populations. Cattails or fish can become abundant in wetlands where water levels have risen to fill more of their topographic basin, and where water-level dynamics have been reduced (Chapters 3 and 4). Consolidation drainage can be indirectly linked to increased abundances of cattails or of fish. Such changes ultimately lead to reduced wetland quality, as defined by the ability to support diverse plant, invertebrate, and waterbird communities.

Restoration of wetlands having various hydroperiods within watershed-derived wetland complexes is likely the most effective approach to reversing the effects of consolidation drainage (Anteau 2012). This strategy entails protection or restoration of temporary and seasonal wetlands encompassed within the catchment of larger wetlands, such as semipermanent wetlands. Conservation programs that purchase land, or gain easements, in areas without direct control over wetland hydrology in the upper-portion of the watershed may be less effective than efforts that directly protect or restore watershed-derived wetland complexes. However, degraded catchments of protected wetlands may receive greater legal attention in the future if land use and wetland drainage are strongly linked to declines in biological productivity and diversity.

Amphipod densities in wetlands across the region remain low compared to historical accounts, despite hydrological conditions that were perceived to be prime for amphipod production during the time of my observations (Anteau and Afton 2008; Chapter 5). Weak evidence suggests that consolidation drainage has had a negative effect on amphipod densities in wetlands. Nonetheless, 23%, 15%, and 6% of wetlands surveyed had >100 amphipods m^{-3} during 2004/05, 2011, and during both 2004/05 and 2011, respectively. This suggests that there are still highly-productive wetlands in the region that provide forage for waterbird populations at various phases within climate variability, and a sparse few wetlands appear to be consistently productive. Further study of wetlands that are consistently highly productive might provide significant insight into factors required for high invertebrate production in wetlands within the region. Such additional research may improve our ability to identify and prioritize these types of wetlands for cost-effective conservation at the landscape scale.

It may prove more useful for waterbird conservation to consider the frequency of highly productive wetlands in the region than to focus on overall mean productivity, or to seek out drivers of small changes in productivity within wetlands. Understanding local and landscape factors that are related to either consistently productive wetlands, or wetlands in which productivity is very dynamic, could help managers understand region-wide levels of productivity through different phases of climate variability. To advance this goal, future research should focus on identifying and intensely studying highly-productive wetlands, while making comparisons to less-productive wetlands. This approach differs from previous regional-scale investigations that typically select subject wetlands randomly, without prior knowledge of system productivity. Such use of prior knowledge has the potential to improve study design, statistical inference, and ultimately our understanding of wetland productivity.

There is potential for characteristics of highly-productive wetlands to be sensed remotely. One such indicator of wetland productivity that can be remotely-sensed is chlorophyll *a* concentration (Chapter 6). My data fail to support the alternative stable state hypothesis due to lack of a bimodal distribution of chlorophyll *a* (Chapter 6). Nevertheless, chlorophyll *a* may be a useful negative indicator of productivity within wetlands as it relates to available waterbird forage, although perhaps within the framework of a continuum. Other indicators of wetland productivity that could be remotely sensed might include vegetation structure, water quality (e.g., turbidity), wetland connectivity, and upland land cover/land use (Naugle et al. 2001). There are several benefits to developing a model of highly-productive wetlands using remotely-sensed data, including increased sample size and spatial distribution, and availability of historic data (e.g., Landsat) to improve capability for time-series analyses. Time-series analyses using remotely-sensed data have the greatest potential to better detect effects of landscape modifications on wetland productivity in the context of climate variability, but this approach will rely on predictions of productivity developed from less extensive studies.

Conservation programs focused on understanding how landscape modifications have altered wetland productivity and that increase the frequency of highly-productive wetlands may better manage long-term wetland quality for waterbirds across different phases of climate variation. Within modified landscapes, recovering a balance between smaller, less-permanent and larger, more-permanent wetlands, linked by through groundwater networks that fluctuate in response to climate variability, will likely enhance waterbird habitat across wet–dry periods of climate fluctuations. Identifying and protecting wetlands exhibiting consistently high levels of productivity can be a more cost-effective model for conservation because these wetlands play a vital role in supporting waterbird populations within the region. Better understanding of what

makes wetlands highly productive will lead to more effective conservation efforts. Such knowledge will be useful in identifying landscapes where complexes of wetlands, with diverse hydroperiods, can be restored potentially creating landscapes that maintain high productivity throughout cycles of climate variability.

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